12-11-2018 12:00 PM

Top-down and bottom-up effects on Collembola communities in soil food webs

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Graduate Program in Biology
A thesis submitted in partial fulfillment of the requirements for the degree in Master of Science

Abstract

Anthropogenic changes are causing shifts within soil food web communities, which may alter ecosystem processes such as nutrient cycling, carbon storage and decomposition. I quantified ecological stressor effects on the abundance, richness, community composition and body size of a soil-dwelling microarthropod (Collembola: Hexapoda). I quantified the effects of warming and nitrogen deposition in two separate field studies and demonstrated that warming shifts Collembola community structure and decreases community body size. I quantified the interactive effects of top-down and bottom-up forces mediated by warming as ecological stressors in Collembola communities. I found that bottom-up effects of nutrient addition did not affect Collembola abundance, richness or community composition, while warming and predator addition interactively reduced abundance and shifted community composition. I demonstrate that top-down and warming effects independently and interactively reduce Collembola density and homogenize community structure. These findings suggest that top-down effects and warming can affect communities in soil food webs and may impact soil ecosystem processes.

Keywords

Body size, Collembola, ecology, nutrient addition, soil food web, top-down effect, warming

Co-Authorship Statement

The work contained in this thesis consists of two collaborative projects. In Chapter 2, soil samples were collected from two experiments in collaboration with Dr. Zoë Lindo and researchers at the Université de Sherbrooke, while Chapter 3 was a collaboration between myself (Jordan Kustec), Carlos Barreto (PhD student), and Dr. Lindo. All data presented in this thesis was completed by myself under the supervision of Dr. Zoë Lindo.

Portions of my research presented in Chapter 2 are incorporated into a submitted manuscript:

- Meehan, M.L., Barreto, C., Kustec, J., Turnbull, M.S., Bellenger, J.-P., Bradley, R., and Lindo, Z. Warming disentangles predator and prey communities in belowground systems. Submitted to *Soil Biology and Biochemistry*.

Co-authors M. Meehan, C. Barreto, M.S. Turnbull and myself contributed to this manuscript by generating data for different taxonomic groups (species identifications and enumeration). Drs. J.-P. Bellenger, R. Bradley, and Z. Lindo were co-principal investigators on the project and collected the samples, while M. Meehan incorporated the taxonomic data into the model used for analyses. M. Meehan wrote the manuscript with input from Z. Lindo and all co-authors. The work presented in this manuscript does not overlap with the work presented in Chapter 2.

The majority of my research presented in Chapter 3 is incorporated into a submitted manuscript:

- Kustec, J., Barreto, C., and Lindo, Z. Warming magnifies top-down control on a soil consumer community. Submitted to *Soil Biology & Biochemistry*.

The experiment was designed by C. Barreto, Z. Lindo, and myself, and the experiment was conducted by C. Barreto and myself. For this manuscript, I generated all the data on the Collembola community, analyzed the data, and wrote the manuscript with input from Z. Lindo and C. Barreto. Further work arising from this experiment may be submitted for publication by C. Barreto as first author in the future.

Acknowledgments

Firstly, I would like to thank my supervisor Zoë Lindo for the immense amount of guidance, dedication and wisdom in her supervision over the duration of my graduate degree. She is unmatched in her dedication towards the success of her graduate students and is otherwise exemplary as a scientist, colleague and mentor.

My fellow lab mates Carlos Barreto, who deserves particular praise for his contributions and leadership to experimental design of Chapter 3, Caitlyn Lyons, Matthew Meehan, Grace Carscallen, Madelaine Anderson, and William Laur, all deserve incredible appreciation for their insight and recommendations for my research. These graduate students, along with those from the Branfireun lab, are also among the most warm-hearted, friendly, caring, and intelligent people I have ever had the pleasure of meeting.

I'd like to also thank the members of my advisory committee Keith Hobson, and Jeremy McNeil. They are highly appreciated for their advice, and critical comments on my thesis document that made this project possible. Part of my thesis obtained data from two field sites near Lac de la Tirasse and Lac Simoncouche in Quebec, both monitored by the University of Quebec at Chicoutimi. Special thanks go to Dr. Jean-Pierre Bellenger, Dr. Robert Bradley, and Dr. Daniel Houle, who facilitated and gave critical insight into the study design.

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Chapter 1

1 Soil food webs and environmental impacts

1.1 Soil system characteristics

The soil food web is responsible for the decomposition of detritus, and the mineralization of nutrients from organic to inorganic forms to become available for plant uptake (Adiscott 2000). The basal resource in soil food webs is detritus, which consists of dead organic matter, from plant litter inputs. As such, the soil food web differs from aboveground terrestrial and aquatic/marine food webs by being primarily 'donor controlled' (Polis & Strong 1996), meaning there is little ability for the feeding behaviour or activity of the consumers to have control or feedback on detrital production. However, the soil food web can be divided into three (or more) distinct trophic levels similar to other food webs: the primary decomposers of detritus, secondary decomposers (and microbial consumers) and predators. The primary decomposers are the first-order consumers of detritus and are largely represented by the soil microbial community composed of bacteria, protozoans, rotifers and fungi (Whalen & Sampedro 2011). Secondary consumers are dominantly microarthropods such as springtails (Collembola) and mites (Acari), but also include enchytraid worms (Enchytraidae), whose body sizes are typically between 150 μm and 1000 μm (Whalen & Sampedro 2011). Both soil predators and secondary consumers control microbial resources through consumption and affect carbon (C) and nitrogen (N) cycling processes (Filser 2002; Thakur *et al.* 2015). The tertiary consumers (i.e. predators) of the system are typically larger than their prey and include predatory mites (Acari: Mesostigmata), centipedes (Chilopoda), and spiders (Araneae).

While decomposition and mineralization processes are mostly due to soil microbes (Van Der Heijden *et al.* 2008), soil fauna enhance these processes through indirect interactions (feeding, dispersing) with the microbial community (Petersen & Luxton 1982). Feeding of mid-trophic level microarthropods on the microbial community can increase respiration (Hanlon & Anderson 1979; Petersen & Luxton 1982) and affect microbial

biomass (Bakonyi 1987) with cascading effects onto decomposition rates and C and N cycling (Moore & Walter 1988; Soong *et al.* 2015). However, this relationship may be unimodal with positive effects of microarthropod grazing only seen at low-intermediate rates, and negative effects observed at high grazing (intermediate grazing hypothesis) (Hanlon & Anderson 1979). The relationships between mid-trophic level microbial consumers and soil predators, particularly in the context of trophic interactions within food webs under environmental change are less well known.

1.2 Environmental change and soil systems

Detritus, especially plant litter, directly contribute to the C stored as soil organic matter (SOM). This SOM is thought to be relatively stable with long residence times (see Cotrufo *et al.* 2015). Consequently, soils store more than twice the amount of C as vegetation (Schimel 1995) and store 80% of the world's carbon (IPCC 2007). As a result, soils are important systems in moderating or mitigating global climate change that is due in part to increasing atmospheric carbon dioxide (CO_2) levels. Warming is predicted to increase average global surface temperatures by 4°C by 2100 (IPCC 2013) primarily due to anthropogenic emissions of greenhouse gasses such as CO_2 and methane. These increases in surface temperatures increase the rates of CO_2 released from soils through enhanced decomposition of SOM due to increased microbial activity (Allison & Treseder 2008). Soil systems under warming increase decomposition rates through changes in the microbial community, specifically shifts from fungal to bacterial dominated systems (Frey *et al.* 2008), and changes in the functional roles of both fungi (Asemaninejad *et al.* 2018) and bacteria (Deslippe *et al.* 2012). The impacts of warming on soil fauna are less well known, however impacts on organism metabolism (Bradford 2013), community body size (Brose *et al.* 2012; Lindo 2015), community composition (Bokhorst *et al.* 2012) and distribution (Garcia-Pichel *et al.* 2013) have been observed. Warming positively effects decomposition, differentially increasing C release from both labile and recalcitrant SOM (Contant *et al.* 2008), altering SOM composition (Pisani *et al.* 2015) and can increase nitrogen mineralization and nitrification rates (Butler *et al.* 2012). Warming also impacts soil food webs, acting as a bottom-up effect (Tuyet *et al.* 2015), and can alter the relative strength of top-down and bottom-up effects (Shurin *et al.*

2012). Mounting evidence suggests that climate warming has altered functional diversity within soil communities (Butler *et al.* 2012; Schwarz *et al.* 2017), which may impact the environmental processes they regulate.

Another global change stressor on ecological communities is increasing nitrogen (N) deposition. Nitrogen deposition rates have increased globally from 34 Tg N $year^{-1}$ in 1860 to 100 Tg N $year^{-1}$ in 1995 (Galloway *et al.* 2004), with rates still increasing due to the use of agricultural fertilizers. For example, the Canadian boreal shield average N deposition rates are 4.27 kg N ha^{-1} yr^{-1} as of 2013 (Hember 2018), and in remote regions these rates are predicted to increase greater than the average global increase (Galloway *et al.* 2004). Increased N deposition can cause soil eutrophication and acidification through the direct deposition of nitric acid and indirectly through acidification reactions within the soil. Soil acidification impacts organisms in soil systems, especially those that are acid intolerant (Stevens *et al.* 2010).

These anthropogenically caused changes have direct effects at the ecosystem level, resulting in perturbations or ecological stressors on organisms. Ecological stressors are biotic or abiotic shifts within ecosystems that affect ecological communities and processes (Alexander 1999). Impacts of ecological stressors are widely studied in terrestrial and aquatic systems (see Vitousek *et al.* 1997; Tylianakis *et al.* 2008). The long-term study of frequent, long-lasting ecological stressors impacts on food webs are relevant to the consistent acceleration of climate warming, N deposition and introduction of new invasive species due to anthropogenic change. Warming impacts can have brief or lasting effects on organism density, which can have cascading effects on trophic interactions and food web stability (Pimm 1982). Ecological stressor impacts are understudied in soil systems despite their previously described importance in global processes. Mounting evidence on global environmental change in soil systems has suggested that soil functionality and biodiversity is being lost (Kibblewhite *et al.* 2008; Briones 2014; Holmstrup *et al.* 2018) with implications for important soil processes. As such, it is important to understand the effects of environmental change on soil systems.

1.3 Predator prey interactions in food webs

Food webs are a complex framework of trophic interactions where predator-prey or consumer-resource interactions transport matter and energy through the food web. Soil food web stability can be affected by physical disturbance through grazing and tilling (Sanchez-Moreno & Ferris 2007), and the aboveground plant community (Bezemer *et al.* 2010), but responses to anthropogenic change and biotic introductions are not well studied. In aquatic systems invasive predators can destabilize food webs through enhanced top-down pressure (Gallardo *et al.* 2016). Other research has shown that some anthropogenic effects magnify the strength of top-down pressure from invasive predators on consumer communities such as nutrient pollution (Wahl *et al.* 2011) and warming (Ingram & Burns 2018) suggesting that the relative forces of top-down effects in soil food webs may respond differently under environmental change.

Another aspect of soil food webs is the relative body sizes of predators and their prey in soil systems. Predator-prey body size relationships serve as an important factor in trophic interactions within a food web and are central factors in food web models (Gravel *et al.* 2013). Predators in terrestrial and aquatic systems are normally larger than the prey items they consume, suggested on average to be twice as large (Hutchinson 1959). In soil food webs this is not always the case. For example, the size of Collembola and their Mesostigmata predators both range from 0.1 to 2 mm (Whalen & Sampedro 2011). The relative impact of warming on size is observed through size-metabolism relationships; increased metabolism of larger predators versus prey can shift community body size (community downsizing) (Lindo 2015). This can further shift the relative strength of predatory interactions and may influence pathways of energy within food webs (Reuman & Cohen 2004). The study of consumer groups within soil systems under ecological stressors can give insight into whether observed trends within terrestrial and aquatic food webs match those of soil food webs.

1.4 Collembola as a model organism in soil food webs

My thesis focuses on Collembola (Hexapoda: Entognatha), a mid-trophic level, abundant, and ubiquitous soil organism. Collembola, commonly known as springtails, are soft bodied, wingless invertebrates that range in body size from 0.1-17 mm. Collembola can be euedaphic (living within the soil), epigeic (living along the soil surface or on vegetation), arboreal or aquatic (Hopkin 1997). Collembola are distributed worldwide, occupying every continent on Earth including Antarctica. There are approximately 8800 described species currently worldwide (Janssens *et al.* 2018) and densities in soil range from 50 to 100,000 individuals per m^2 (Petersen & Luxton 1982; Ponge *et al.* 1997). Collembola, as soft bodied animals, are vulnerable to predation by soil predators such as centipedes and mesostigmatid mites (Bruckner *et al.* 2016), but many possess a specialized forked organ called a furcula, which helps them escape predation by springing away from predators. Generally, Collembola are opportunistic, generalist consumers of the soil microbial community, feeding on bacteria, protozoa and fungi (Chahartaghi *et al.* 2005), although stable isotope analysis has shown a wide range of feeding groups (Chahartaghi *et al.* 2005). Collembola can also accelerate microbial dispersal by transporting fungal spores attached to their cuticle to new soil substrates (Visser *et al.* 1987).

Collembola are particularly vulnerable to shifts in environmental variables, such as soil moisture (Krab *et al.* 2013), warming (Bokhorst *et al.* 2012) and nutrient availability (Ochoa-Hueso *et al.* 2014). Consequently, they are often used as bioindicators of soil and habitat quality (Cassagne *et al.* 2006) making them an important model organism and functional group to study in the context of anthropogenic change. However, different Collembola species may respond to global change factors depending on their morphological traits (e.g. body size). Collembolan body size is a morphological trait that is often correlated with reproductive strategy (e.g. asexual vs sexual reproduction), euedaphic vs epigeic, drought resistance, predation risk or feeding preference (Hopkin 1997). Morphological traits are increasingly being used as proxies for functional traits, which are morphological and physiological characteristics that place species to an

ecological role within an ecosystem (Díaz *et al.* 2013). For instance, the absence of furcula and eyes are commonly used as a proxy to identify soil dwelling Collembola that persist in smaller habitat ranges, and that primarily consume mycorrhizal fungi (Jonas *et al.* 2007). Soil dwelling Collembola are often smaller bodied and are more commonly parthenogenetic, while larger bodied Collembola are surface, litter or arboreal dwelling, consume saprotrophic fungi and are sexually reproductive (Jonas *et al.* 2007).

1.5 Thesis rationale and overview

In this thesis I studied how warming, nutrient addition, including nitrogen deposition, and predator addition change Collembola communities in boreal forest systems. I examined these factors individually and interactively as ecological stressors and to examine the impacts on food webs. Collembola were chosen as an ecological model organism due to their presence, diversity and importance in soil processes. I conducted a field and a laboratory study, manipulating environmental variables associated with global change. In the first experiment (Chapter 2) I focused on the effects of intense soil warming and multi-level increases in N deposition on Collembola communities in two field experiments in the Canadian boreal forest. Warming treatments were direct soil warming increases of 4°C to simulate predicted increases in soil temperatures due to climate warming (IPCC 2013). Nitrogen deposition treatments represent the predicted increase in atmospheric N deposition due to intensification of agriculture and fossil fuel combustion globally (Galloway *et al.* 2004). To assess the effects of these ecological stressors on Collembola communities, I measured species abundance, species richness, species diversity, community compositional shifts, and community body size distributions under the different treatments.

In my second study (Chapter 3) I focused on the interactive effects of soil warming, increases in available nutrients, and increased predator addition on Collembola communities in a full factorial laboratory soil mesocosm study. The nutrient addition treatment was performed to strengthen bottom-up trophic controls and simulating agricultural inputs of fertilizer. The predator addition treatment was performed to strengthen top-down trophic controls, simulating biological invasions or biocontrol of

predator species in many ecosystems. The warming treatment was performed partially to additionally strengthen the bottom-up trophic control on the Collembola community, but also to assess the interactive effects of warming on both bottom-up and top-down controls. These interactive effects are important to examine because there will be increases in soil temperature due to climate warming in systems already subject to other anthropogenic changes. To assess shifts in bottom-up and top-down control on Collembola communities, I measured Collembola species abundance, species richness, species diversity, and community composition. Chapter 4 summarizes the results of my experimental work (Chapters 2 and 3) and places the in the context of previous literature to discuss how both collembolan and other ecological communities may shift due to anthropogenic change. Finally, I discuss how multiple environmental changes may interact in the future to affect both soil communities and soil ecosystems.

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Chapter 2

2 Ecological stressor impacts on boreal forest soil communities

2.1 Introduction

2.1.1 Environmental changes as ecological stressors

Shifts in environmental variables can act as ecological stressors to communities within ecosystems. Leading ecological stressors affecting ecological communities globally include land-use change (e.g. forest-agriculture-urban transitions), changes in climate (e.g. warming and precipitation patterns), nitrogen deposition, invasive species, and increasing atmospheric CO_2 (Sala *et al.* 2000). These stressors lead to changes in community composition and often, losses in species richness. Different categories of ecological stressors (Sutherland & Menge 1987) result in losses of fauna diversity, biomass and composition with different mechanisms (Thakur *et al.* 2015). For instance, climatic stressors such as warming can induce thermal stress on organisms or can affect abiotic factors such as moisture within soils (Samaniego *et al.* 2018). Nitrogen deposition and other types of pollution can also act as an ecological stressor through direct toxicity (Boxman *et al.* 1998), or by affecting the growth of plant and microbial communities through nutrient loading (Van der Heijden *et al.* 2008; Koorem *et al.* 2014). Ecological stressors reshape ecological communities in aboveground and aquatic systems, as well as belowground (soil) systems. While the soil substrate itself provides some protection from many ecological stressors through insulation and acting as a buffer (Bowman *et al.* 2008), soil organisms whose entire life cycle is spent within the soil are affected by climatic (Kennedy 1994; Jucevica & Melecis 2006) and pollution stressors (Boxman *et al.* 1998). For instance, while soil temperature only increases a fraction of the rise in air temperature, soil warming is a stressor responsible for community shifts (Jucevica & Melecis 2006) but is dependent on soil type and depth (Zheng *et al.* 1993).

Ecological stressors may also differentially affect communities depending on the length of exposure; e.g., short disturbance events like fire and flooding compared to long-term ecosystem level or global shifts like warming and nitrogen deposition. Soil fauna can be

resilient to some short-term ecological stressors (Čerevková *et al.* 2013; Krab *et al.* 2014) but greatly affected by others (Bokhorst *et al.* 2013; Holmstrup *et al.* 2018). However, these communities may potentially be more vulnerable to long-term climate change and pollution stressors (Jucevica & Melecis 2006; Rzeszowski *et al.* 2017). The impact of long-term stressors will vary depending upon the ecosystem but there are few studies examining the effects on soil fauna (but see Malmström 2012; de Vries *et al.* 2012).

2.1.2 Ecological stressors impact boreal forest soil fauna

The boreal forest covers 17% of the world's land surface and is geographically located between temperate forests and tundra (Brandt 2009). Dominant vegetation within the boreal forest ecosystem includes pines, spruces, shrubs, fir, tamarack, lichens with mosses as ground cover (Brandt 2009). The boreal forest is the largest forest system in Canada comprising 25% of Canada's land cover and 72% of its forest area (Brandt 2009). Consequently, the boreal forest system is vital in global carbon storage, air filtration, water storage and nutrient cycling, providing a vast amount of other ecosystem services and resources from harvesting. It is important to know the impact of harvesting and anthropogenic driven shifts in climate and pollution on organisms and the ecosystem services they provide (Lemprière *et al.* 2008; Pohjanmies *et al.* 2017). Nitrogen (N) deposition can affect both tree and moss species in boreal systems, eliciting aboveground changes that impact soil properties (Ackermann *et al.* 2012; Armitage *et al.* 2012). The predicted 1-2°C change in temperature with even greater increases overwinter (IPCC 2013), will have severe effects on ecosystems in northern latitudes such as the boreal forest.

The known effects of increased N deposition for boreal forest regions mostly relate to plant community shifts and increased acidity associated with reactive atmospheric N (e.g. NO_x). Specifically, total moss cover decreases under nutrient, and especially N addition (Gunnarsson *et al.* 2004). Moss cover is an important habitat for soil surface dwelling microarthropods (i.e. Collembola and mites) (Sereda *et al.* 2012), as well as for maintaining soil moisture content (Meingast *et al.* 2014), temperature insulation (Soudzilovskaia *et al.* 2013), habitat connectivity (Saraeva *et al.* 2015) and food resources (Krab *et al.* 2013) for soil organisms. Similarly, climate change is affecting

boreal forest systems (Mazziotta *et al.* 2016), with most studies examining the response of tree species (Lemprière *et al.* 2013), soil buffering capacity (Bowman *et al.* 2008) and the response of smaller organisms such terrestrial arthropods to climate change (Volney & Fleming 2000).

Collembola (springtails) are soil and soil surface dwelling microarthropods that are resilient to some ecological stressors (e.g. drought & fire) (Lindberg & Bengtsson 2006; Gongalsky & Persson 2013), but display negative responses in diversity and biomass, alongside community shifts when exposed to other stressors such as warming and flooding (Lindberg & Bengtsson 2006; Turnbull & Lindo 2015). For instance, in a decade long study of Scots pine (*Pinus sylvestris* L.) forest stands, Jucevica & Melecis (2006) found that soil dwelling Collembola were negatively affected by an increase in air temperature. However, Alatalo *et al.* (2015) found no effect of warming on Collembola after two decades in a subarctic plant system. In another long-term study, Bokhorst *et al.* (2008) found reduced Collembola diversity inhabiting arctic lichen under warming, but not in moss or dwarf grass communities. Furthermore, these losses in diversity are not easily recovered by new colonizers due to the low dispersal ability of soil microarthropods and specifically euedaphic (true soil dwelling) Collembola (Bengtsson *et al.* 2002; Dunger *et al.* 2002).

2.1.3 Community body size responses to ecological stressors

Warming can increase metabolic costs for organisms (Brown *et al.* 2004), a relationship that varies depending on body size and trophic position. Specifically, increased metabolic costs are greater for larger bodied, higher trophic level organisms, and warming has been shown to result in smaller bodied individuals in aquatic systems (Sheridan & Bickford 2011). While warming impacts on body size relationships are relatively understudied in soil fauna, historical data shows that climate warming during the Paleocene-Eocene Thermal Maximum correlated with smaller body sizes in soil microarthropods (Smith *et al.* 2009). Warming also favours small bodied oribatid mite species (Lindo 2015).

In most communities, the relationship between species abundance and the average body size of a species is negative, such that when both abundance and body size are plotted on a logarithmic scale the negative relationship is linear with an observed slope of approximately -0.75 (Blackburn *et al.* 1993). This relationship is referred to as the body size spectra — log-transformed species abundance values on the y axis and log-transformed species body masses (or sizes) on the x axis (Petchey & Belgrano 2010). Because body size, as a morphological trait, has been linked to trophic position, and metabolic rates (Woodward *et al.* 2005), it is expected that different body-sized species will respond differently to ecological stressors, and a shift in the body size spectra will be observed. Increases in the abundance of small-bodied species (Lindo 2015) or losses in the abundance of large-bodied species (Staddon *et al.* 2010) will lead to a steepening of the slope of this relationship. This phenomenon, referred to as 'community downsizing', represents a decrease in the average body size in the community, and this has been suggested to relate to changes in energy transfer from one trophic level to another (Petchey & Belgrano 2010). Body size considerations in food webs have mostly focused on size-structured trophic interactions (Andersen *et al.* 2009), but more recently are incorporating energetic (Ehnes *et al.* 2014) and stoichiometric (Ott *et al.* 2014) aspects to understanding overall community structure. Mechanistic understanding of predator-prey (or consumer-resource) interactions while incorporating body size may also link community structure to ecosystem level functions such as litter decomposition and nutrient dynamics (Schneider *et al.* 2012). Thus, body size is an easily determinable functional trait that may provide a powerful tool for analysis of soil community structure and ecosystem function under environmental change scenarios (Turnbull *et al.* 2014).

2.1.4 Objectives and predictions

The objective of my research was to assess changes in Collembola community (richness, abundance, body size, and composition) under single factor ecological stressors of warming and N deposition in two separate field studies over a three-year time period. I hypothesize that Collembola richness and abundance will be reduced and community composition more homogenous under warming due to losses in specific species under thermal stress. I predict that community body sizes will decrease under warming as

higher temperatures provide conditions more favourable for the proliferation of smaller bodied species. Under N deposition, I hypothesize that Collembola richness and abundance will also decrease due to loss of moss cover and communities will become more homogenous due to a loss of surface-dwelling species. I predict that the average community body size will decrease due to a loss of moss cover, which is the primary habitat for larger bodied epigeic Collembola.

2.2 Materials & methods

2.2.1 Study site and sampling design

2.2.1.1 *Simoncouche watershed: Warming experiment*

Boreal forest floor samples were collected from a warming experiment near Lac Simoncouche (48°13′N, 71°15′W) in the Laurentides Wildlife Reserve approximately 30 km south of Saguenay, Quebec, Canada. Average temperature in this region is 1.4°C while precipitation is approximately 860 mm annually (La Baie station, data 2000-2018, Environment Canada 2018). The dominant vegetation is black spruce (*Picea mariana* (Mill.) B.S.P.) and carpets of the feather moss *Pleurozium schreberi* (Brid.) Mitt. The experimental set-up consisted of 16 circular open-top chambers, 1 m in height and 165 cm diameter. Half the chambers were not heated ($T_{control}$), while in the other half the soil temperature was increased by +4°C (T_{warm}) relative to soil outside the chambers, induced by heating cables placed 20 cm below the surface of the moss layer. Warming conditions are based on a moderate climate change prediction for the region in the next 50-100 years (IPCC, 2013). Forest floor soil core samples (5.5 cm diameter) of the surface mosses, as well as organic and mineral soils were collected to a depth of 10 cm from each chamber in July 2015, July 2016 and in October 2017. Samples were kept at 4°C in individual soil corers and extracted within 72 hrs of sample collection.

2.2.1.2 *Tirasse watershed: Nitrogen deposition experiment*

Boreal forest floor samples were collected from a long-term nitrogen deposition site near Lac de la Tirasse (49°12′45′N 73°39′00′W) in the Ashuapmushuan Wildlife Reserve 231 km northeast of Saguenay, Quebec, Canada. The average annual temperature in the

region is 1.1°C while total annual precipitation is approximately 860 mm (Chamouchouane station, data 1994-2018, Environment Canada 2018). The dominant vegetation is black spruce (*P. mariana*), jack pine (*Pinus banksiana* Lambert 1803) and mosses (*P. schreberi*) covering the forest floor. Precipitation was collected weekly from 1997 to 2012 for analysis of inorganic N concentrations, from which N deposition treatments are derived (see Houle & Moore 2008 for more details). The concentrations of NO_3 and NH_4 in precipitation were determined through ion chromatography and colour calorimetry with a Technicon AA2, respectively, and average total N deposition rates during this period were determined to be 3.0 kg ha^{-1} $year^{-1}$ (Houle & Moore 2008). Nine experimental plots (10 m × 10 m) were established in the year 2000 with three experimental N treatment levels. Plots were either treated with no additional nitrogen beyond natural deposition ($N_{control}$), five (N_{5x}), or ten (N_{10x}) times the average N deposition rate. Additional N deposition was applied using a backpack sprayer each month during the growing season (May to September) with a NH_4 and NO_3 solution dissolved in deionized water as described in Houle & Moore (2008). Forest floor soil core samples (5.5 cm diameter) of the surface mosses, and organic and mineral soils were collected to a depth of 10 cm of each plot in July 2015, July 2016 and in October 2017. Samples were kept at 4°C in individual soil corers and extracted within 72 hrs of collection.

2.2.2 Sampling processing

Soil fauna were extracted from core samples collected from both sites using Tullgren funnels, where a heat and desiccation gradient actively drives microarthropods downward into a 75% ethanol preservative over 72 hrs. Extracted Collembola were enumerated and identified to species level where possible using the keys of Christiansen & Bellinger (1998). Total and species level abundances were standardised per 10 g dry weight soil. Collembola from 2015-2016 were initially enumerated and morphotyped by M. Turnbull, while I performed species identifications, and enumerated and identified samples collected in 2017. I re-examined 2015-2016 data to ensure consistency across all years. Soil moisture of core samples from both experiments was measured gravimetrically by

measuring the initial soil wet weight and the post fauna extraction soil dried weight, and calculated using the following equation:

$$\text{Moisture content (\%)} = ((\text{wet weight (g)} - \text{dry weight (g)}) / \text{wet weight (g)}) \times 100.$$

2.2.3 Data analysis

Collembola diversity was calculated using Shannon's diversity (H') and Pielou's evenness (J) for each sample using the {vegan} package in R (version 3.1.2; R Development Core Team). Total standardised Collembola abundance and richness, Shannon's diversity and Pielou's evenness were initially evaluated for the main treatment effects (warming or N deposition) using repeated measures analysis of variance (RM-ANOVA) across all time points. Large yearly differences were apparent for both datasets, so subsequent ANOVAs were used to observe within year treatment effects.

The Collembola community composition was analysed using Bray-Curtis measures of dissimilarity for standardised abundances of Collembola species with a Hellinger transformation. Collembola community composition was visualised using non-metric multidimensional scaling (NMDS) in R using the {metaMDS} function, and the significance of dissimilarity for main treatment effects was performed with permutational ANOVA (PERMANOVA) using the {adonis} function in R. For the NMDS, the final ordination presents dissimilarities in species composition between samples; data points that are further away from each other represent samples that are more dissimilar in community composition than data points that plot closer together. For the Simoncouche warming experiment all years were grouped for community analyses as community variation was low despite yearly effects on richness and abundance. For the Lac Tirasse N deposition experiment yearly datasets were analysed separately because community composition was highly heterogeneous among years. Similarity of percent analysis (SIMPER) was conducted using the SIMPER package in PRIMER 5 (PRIMER-E Ltd., 2001) to quantify within treatment similarity and among treatment dissimilarity, and to assess which species contributed the most to compositional shifts. Hellinger transformed community data were also used in a Principal Components Analysis (PCA) to examine species driven compositional trends. Subsequent ANOVAs were used on sample factor

scores from the PCA to determine whether treatments were significantly related to Collembola composition.

Representative adult specimens for each species (up to 10 individuals, or all individuals when total abundance was <10) were slide mounted and measured for total body length (μm) under 200-400× magnification. Body length measurements were transformed to body sizes (dry weights) using the power function:

$$\text{Body mass } (\mu g) = (b \times L(mm))^3$$

where L is measured body length in mm, and b is equal to a family specific constant as found in Edwards (1967). Slopes of the relationship between log transformed abundances of species and their body sizes were built with a 50% quantile regression and treatment effects on the slope and intercept were analyzed with an ANOVA with data from all years pooled.

2.3 Results

2.3.1 Simoncouche warming experiment

A total of 3113 Collembola from 38 species were counted and identified from 2015-2017 Simoncouche soil samples (Appendix 2.1). Warming treatments did not significantly decrease the moisture content of the soils ($F_{1,43}$=0.63, p=0.431), but year effects on moisture content were present ($F_{2,44}$=18.0, p<0.001), where 2016 had lower moisture contents. The average Collembola abundance and species richness in 2015 was 31.2 individuals (±2.6 SE) and 5.0 species (±0.2) per 10 g dwt, respectively. The average Collembola abundance and species richness in 2016 was 44.4 (±1.6) individuals and 7.5 species (±0.2), and in 2017 was 74.1 (±2.6) individuals and 8.37 species (±0.2) per 10 g dwt. Collembola species richness significantly increased from 2015 to 2017 (richness: $F_{2,44}$=4.96, p=0.011) (Figure 2.1A). Richness was not affected by warming treatments ($F_{1,45}$=0.05, p=0.825), and there were no significant interactions between year and warming treatments ($F_{2,26}$=0.52, p=0.600). Similarly, Collembola species abundance significantly increased from 2015 to 2017 ($F_{2,40}$=4.35, p=0.020) (Figure 2.1B), but was not affected by warming ($F_{1,45}$=0.05 p=0.831), there were no significant interactions

between year and treatment effects ($F_{2,26}$=0.77, p=0.469). Shannon's diversity index significantly increased from 2015 to 2017 ($F_{2,44}$=15.68, p<0.001) without a change in evenness ($F_{2,44}$=1.23, p=0.302) (Table 2.1), and warming treatments significantly increased Shannon's diversity index ($F_{1,45}$=6.04, p=0.018) and Pielou's evenness ($F_{1,45}$=5.80, p=0.020) (Table 2.1).

Community structure was significantly different among sampling years ($F_{2,44}$ = 3.54, p=0.001) while 2015 and 2016 were similar in community space, 2017 showed patterns of homogenization (*i.e.* clustered more closely in ordination space) and was nested within 2015 (Figure 2.2). Warming was also a significant factor in structuring Collembola communities when years were pooled ($F_{1,46}$ =3.23, p=0.002), with 2016 being highly significant in this trend ($F_{1,14}$=3.23; p=0.006). Overall communities became more similar over time, with average similarity increasing from 30.2%, to 34.1%, to 42.7% over 2015, 2016 and 2017, respectively. *Folsomia penicula* Bagnall, 1939, contributed 72.2% to the similarity among samples in 2015, 49.5% in 2016, and 43.7% in 2017. Species in the family Onychiuridae also contributed to within year similarity trends, with *Onychiurus* sp. 1 and Onychiuridae sp. 2 contributing a combined 14.1% similarity in 2015, and 22.8% in 2017, while *Sensiphorura* sp. 1, Onychiuridae sp. 1 and Onychiuridae sp. 3 contributed a combined 27.2% similarity in 2016.

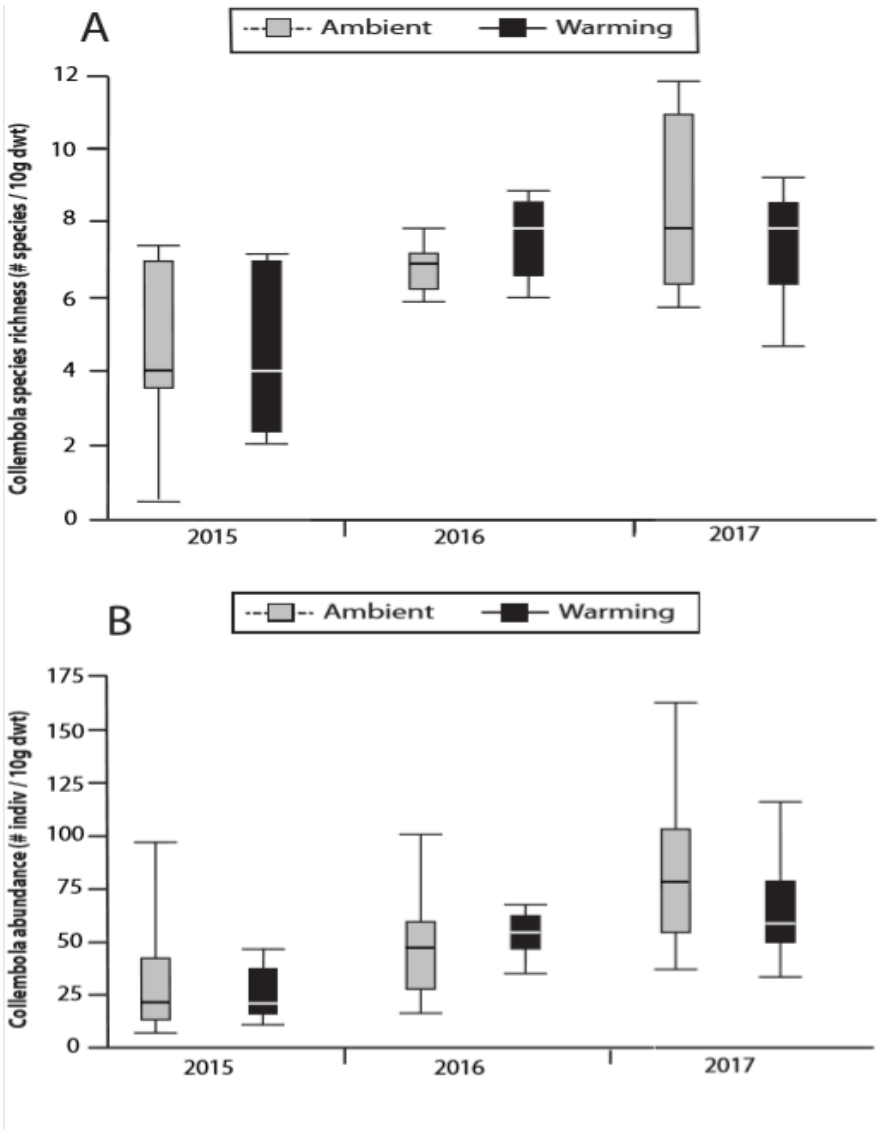

Figure 2-1 The species richness (A) and abundance (B) of Collembola under warming in Simoncouche Quebec from 2015 to 2017

Standardized richness for Collembola A) species richness (# species / 10 g dwt) and B) abundance (# individuals / 10 g dwt) across sampling years 2015, 2016 and 2017 at Simoncouche. Boxes represent sample ranges with means as white and black lines with bars displaying 95% confidence intervals.

Table 2-1 Shannon's diversity and Pielou's evenness index values of Collembola under warming in Simoncouche Quebec

Diversity indicator	Ambient	Warming	$F_{1,45}$	p
Shannon diversity (*H'*)	1.30(0.09)	1.62(0.09)	6.04	**0.018**
Pielou's evenness (*J*)	0.36(0.02)	0.44(0.03)	5.80	**0.020**

Values are derived using Collembola communities standardized by 10 g dry weight. Values are means across 2015 to 2017 with standard error in parentheses.

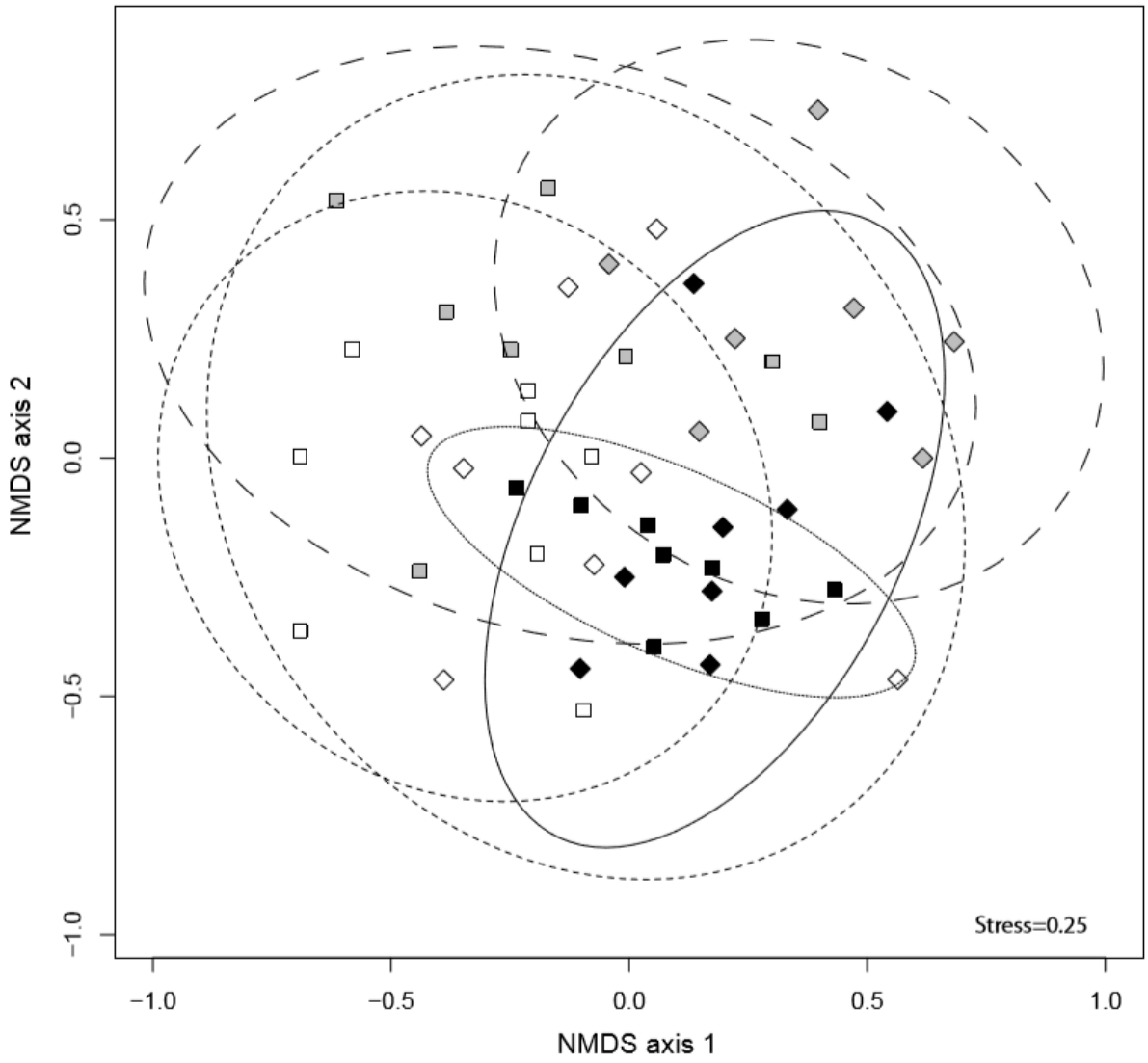

Figure 2-2 Nonmetric multidimensional scaling (NMDS) ordination biplots displaying Collembola community composition under warming in Simoncouche Quebec from 2015-2017

Data points represent communities for individual samples collected from the Simoncouche warming experiment. White, grey and black symbols represent years 2015, 2016, and 2017 respectively, while squares and diamonds represent ambient and warmed communities. Ellipses are 95% confidence intervals with dotted, hatched and solid ellipses representing those that bind 2015, 2016, and 2017 communities respectively.

Communities became less similar (more heterogeneous) under warming, with average similarity decreasing from 32.6% under ambient treatments to 30.4% under warming treatments. *Folsomia penicula* contributed to 71.8% similarity between communities under non-warmed conditions and 44.5% under warming conditions. Species within the family Onychiuridae also contributed to among sample similarity for ambient and warmed treatments, with *Onychiurus* sp. 1 and Onychiuridae sp. 3 contributing a combined 11.0% similarity in ambient communities, while *Sensillonychiurus eisi* (Rusek, 1976), Onychiuridae sp. 1 and Onychiuridae sp. 3 contributed a combined 30.3% similarity among warming treatments.

The PCA of the Collembola community across all years suggests that year effects were strong in structuring community composition. Both PC axis 1, explaining 10.6% of variation, and PC axis 2, explaining an additional 10.0% of the variation, were significantly related to sampling year (PC1 Year: $F_{2,44}=20.02$, $p<0.001$; PC2 Year: $F_{2,44}=10.90$, $p<0.001$), and were not related to warming treatment effects (Figure 2.3). Negative values on PC axis 1 represent species occurrences associated with sampling in 2016, specifically *Sensiphorura* sp. 1, *Pseudosinella dubia* Christiansen, 1961 and *Onychiurus* sp. 2 having high negative scores. Positive values on PC axis 1 represented species occurrences in sampling years 2015 and 2017, with *Tetracanthella ethelae* Wray, 1945 and *Tomocerus* sp. having high positive scores. Similarly, negative values on PC axis 2 represent species found in 2015 and 2016 sampling years with *Arrhopalites incertus* Zeppelini & Christiansen, 2003, *Folsomia regularis* Hammer, 1953, *Metisotoma grandiceps* (Reuter, 1891) having high negative scores. Positive values for PC axis 2 represent species sampled in 2017, where *Taffalia* sp. 1, *Hypogastrura nivicola* (Fitch, 1847), *Brachystomella stachi* Mills, 1934 and *S. eisi* had high positive scores.

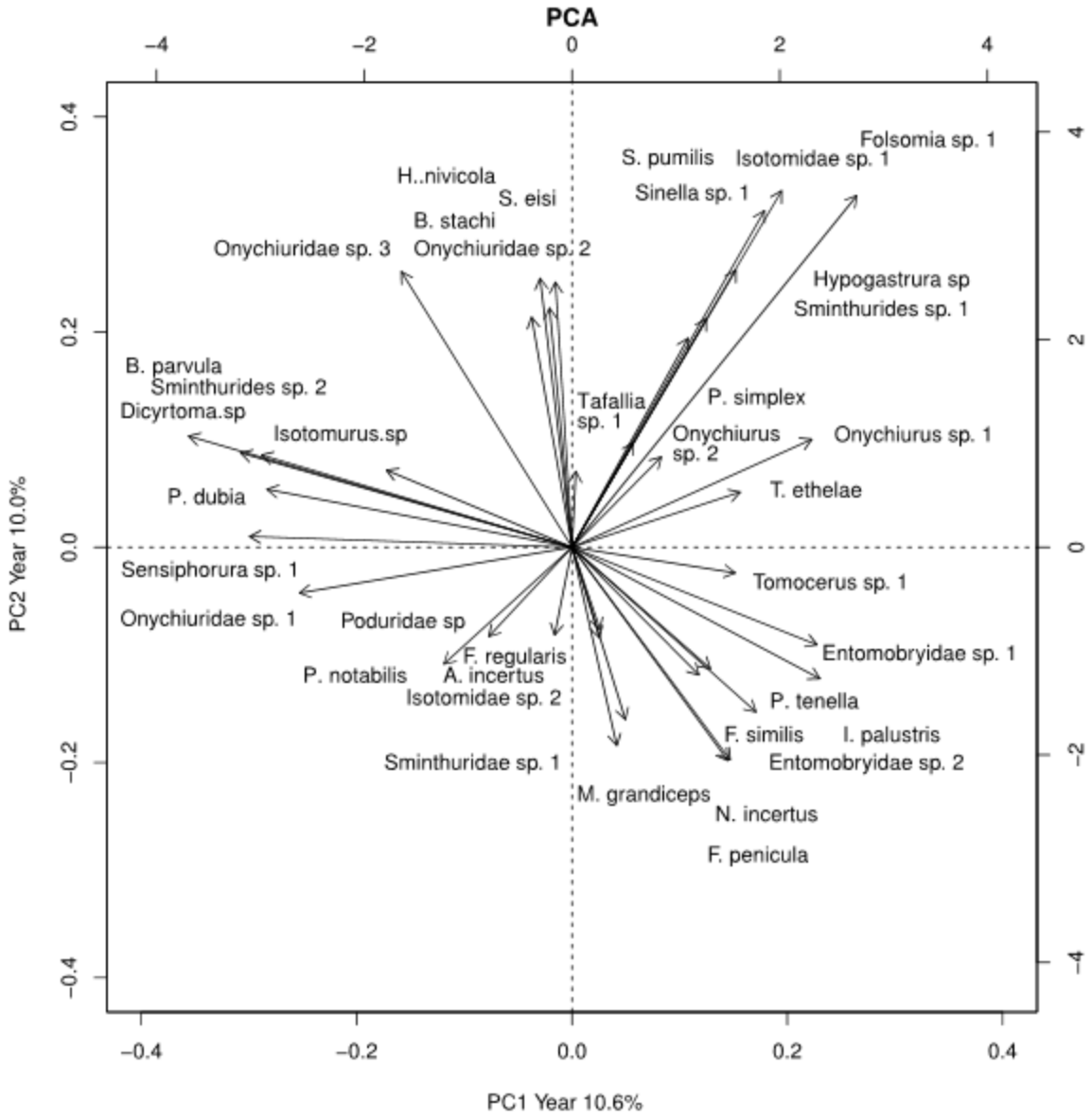

Figure 2-3 Principal component analysis (PCA) of Collembola communities across three years under a warming in Simoncouche Quebec

Both PCA axes were explained by year effects, with negative values on PC axis 1 being species driven by year 2016, and positive values years 2015 and 2017. Negative values on PC axis 2 are explained by years 2015 and 2016 while positive values are explained by year 2017.

The body size spectra analysis showed that warming treatments increased the intercept and steepened slope of this relationship compared to ambient conditions (Figure 2.4), but the effect was not significant (temperature: $F_{1,31}$=1.90, p=0.177). This trend was in part due to an increase in small bodied Onychiurid species such as *Onychiurus* sp. 1, Onychiuridae sp. 1, sp. 4 and sp. 6, and a small increase in mid-sized species such as *Proisotoma tenella* (Reuter, 1895), Entomobryidae sp. 2 and *Isotomurus palustris* (Muller, 1776). *Folsomia penicula* was excluded from this analysis because there was a vast difference in body size between adults and juveniles, with overall body sizes ranging from 0.06-0.49 μg. No other species displayed such a wide variation in body size.

2.3.2 Tirasse nitrogen deposition experiment

A total of 2513 Collembola across 40 species were counted and identified from 2015-2017 Tirasse soil samples (Appendix 2.2.) The average Collembola abundance and species richness in 2015 was 17.9 individuals (±3.0 SE) and 3.8 species (±0.6) per 10 g dwt, respectively. The average Collembola abundance and species richness in 2016 was 86.3 (±20.0) individuals and 11.1 species (±1.2), and in 2017 was 59.1 (±15.1) individuals and 7.3 species (±1.0) per 10 g dwt. Nitrogen deposition treatments ($N_{Control}$, N_{5x} and N_{10x}) did not significantly affect species richness ($F_{2,29}$=0.90, p=0.419), abundance ($F_{2,29}$=0.36, p=0.700), Shannon's diversity index ($F_{2,29}$=2.47, p=0.102), or evenness ($F_{2,29}$=0.64, p=0.535). Similar to the Simoncouche warming experiment, significant among year effects were observed, with 2015 having significantly lower species richness ($F_{2,29}$=14.02, p<0.001) and abundances ($F_{2,29}$=8.36, p=0.001) than in subsequent years (Figure 2.5). In 2015, Shannon's diversity was also significantly lower ($F_{2,29}$=2.79, p=0.078), but there were no significant differences between years for measures of evenness (Year: $F_{2,29}$=2.47, p=0.102) (Table 2.2). There were no significant interactive effects between N deposition treatments and sampling year for richness and abundance (richness: $F_{4,10}$=0.85, p=0.525, abundance: $F_{4,10}$=1.09, p=0.412).

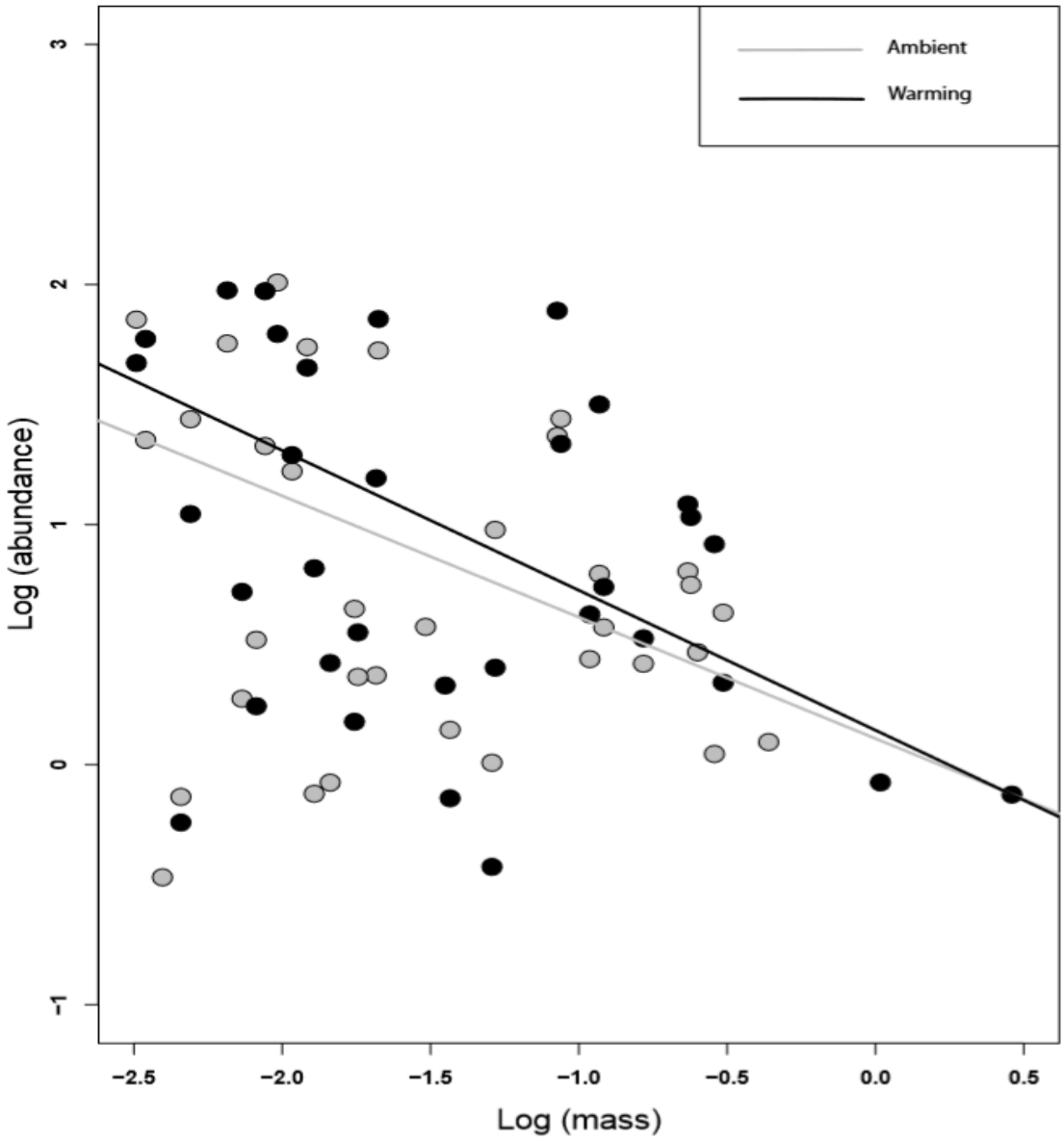

Figure 2-4 Body size spectra (BSS) of Collembola communities exposed to warming in Simoncouche Quebec

Log transformed Collembola species mass (μg) and standardised abundance (# individuals / 10 g dwt) for temperature treatment relationship across all sampling years in the Simoncouche experiment. Grey and black dots and lines represent ambient and warmed species abundances and body size spectra slopes respectively.

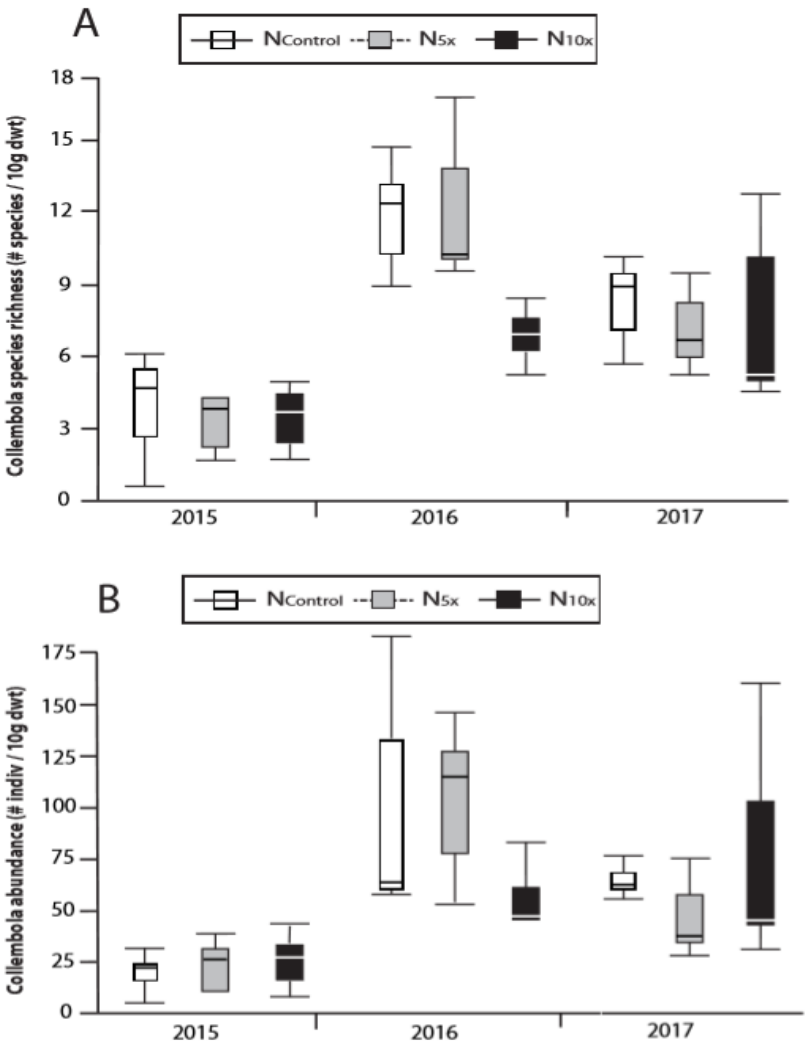

Figure 2-5 Richness and abundance of Collembola in response to nitrogen deposition in Tirasse, Quebec from 2015-2017

Standardized Collembola A) species richness (# species / 10 g dwt) and B) abundance (# individuals / 10 g dwt) across sampling years 2015, 2016 and 2017 for Tirasse samples. Boxes represent sample ranges with means as white and black lines with bars displaying 95% confidence intervals. $N_{control}$, N_{5x}, and N_{10x} refer to treatments of no added N deposition, five times and ten times normal N deposition rates in the area respectively.

Table 2-2 Shannon's diversity and Pielou's evenness index values of Collembola communities under nitrogen deposition in Tirasse, Quebec

Diversity indicator	$N_{control}$	N_{5x}	N_{10x}	$F_{2,29}$	p
Shannon diversity (*H'*)	1.57(0.05)	1.75(0.15)	1.61(0.15)	0.36	0.700
Pielou's evenness (*J*)	0.43(0.01)	0.48(0.02)	0.44(0.02)	2.47	0.102

Values are derived using Collembola communities standardized by 10 g dry weight. Values are means across 2015-2017 with standard error in parentheses.

I found strong year effects within the study that led to communities being highly and significantly different between years ($F_{2,30}$= 7.43, p<0.001) (Figure 2.6). Treatments of N deposition significantly structured communities in 2015 ($F_{2,11}$=1.99, p=0.004) with N_{5x} and N_{10x} communities being dissimilar to $N_{control}$ communities and more heterogeneous (Figure 2.7). In years 2016 and 2017 N deposition did not have a significant effect in structuring communities (2016: $F_{2,8}$=1.14, p=0.360; 2017: $F_{2,8}$=0.63, p=0.895). Similarly, using PCA, I found that species composition in 2015 was marginally related to N deposition (Figure 2.8). The PC axis 1 explained 17.0% of the variation in community composition and was related to N deposition ($F_{2,11}$=3.65, p=0.061) with negative values related to $N_{control}$ conditions and positive values for PC axis 1 related to N_{5x} and N_{10x} deposition treatments. Species associated with $N_{control}$ conditions were *I. palustris*, *Hypogastrura* sp., and Onychiuridae sp. 1, while the main species related to N deposition treatments was *M. grandiceps*.

Nitrogen deposition treatments did not significantly affect the slope of the body size spectra compared to control treatments ($F_{2,27}$=2.234, p=0.146) (Figure 2.9), although the N_{5x} treatments had a shallower slope due to the prevalence of some mid-sized Collembola (e.g. *Parisotoma notabilis* (Schaffer 1896), and *F. regularis*) compared to the control. *Folsomia penicula* was also excluded from this body size spectra analysis due to its wide range of body sizes.

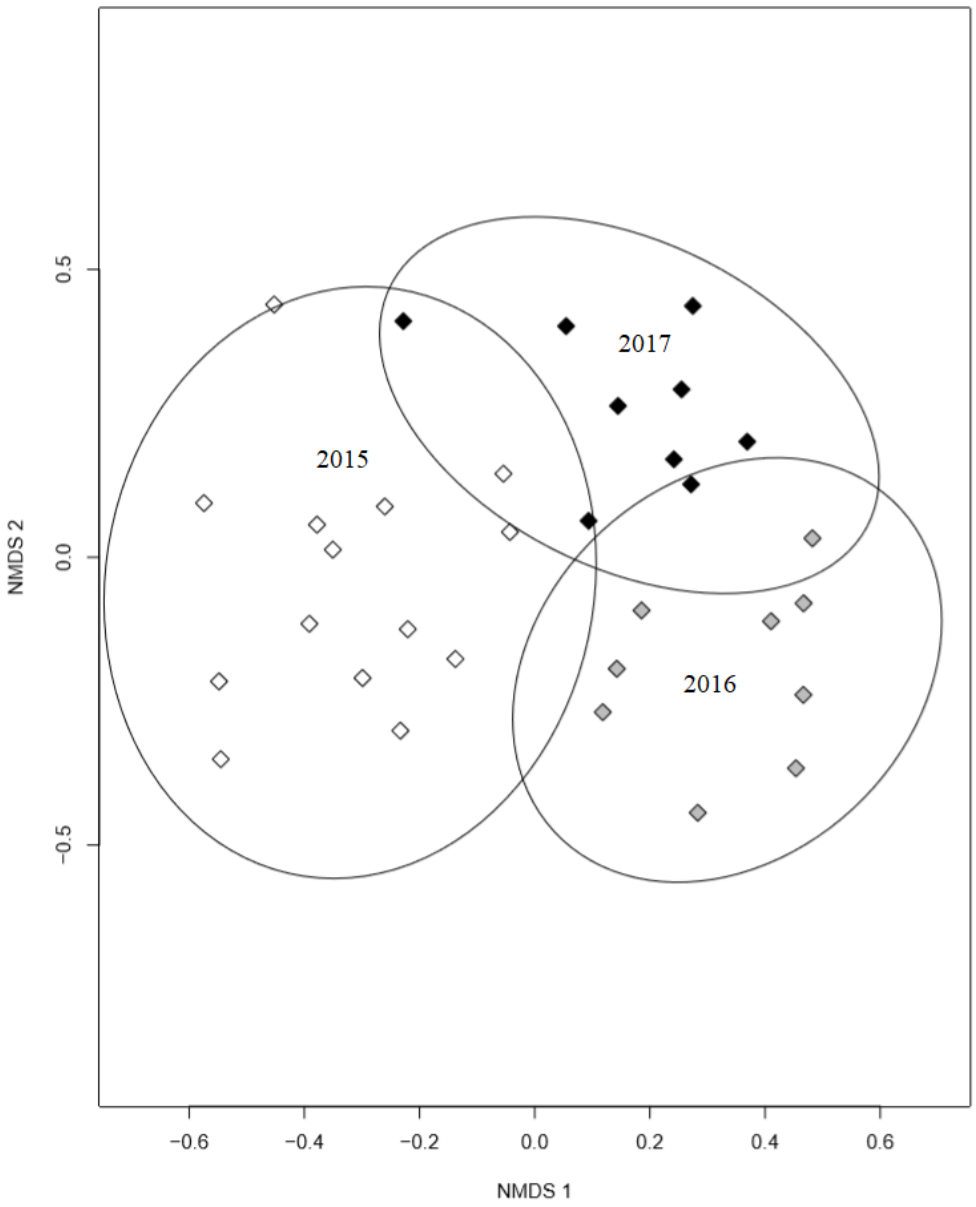

Figure 2-6 Nonmetric multidimensional scaling of Collembola communities across three years in Tirasse, Quebec

Data points represent communities for each soil sample. White, grey and black diamonds represent communities in 2015, 2016 and 2017 respectively. The ellipses are 95% confidence intervals.

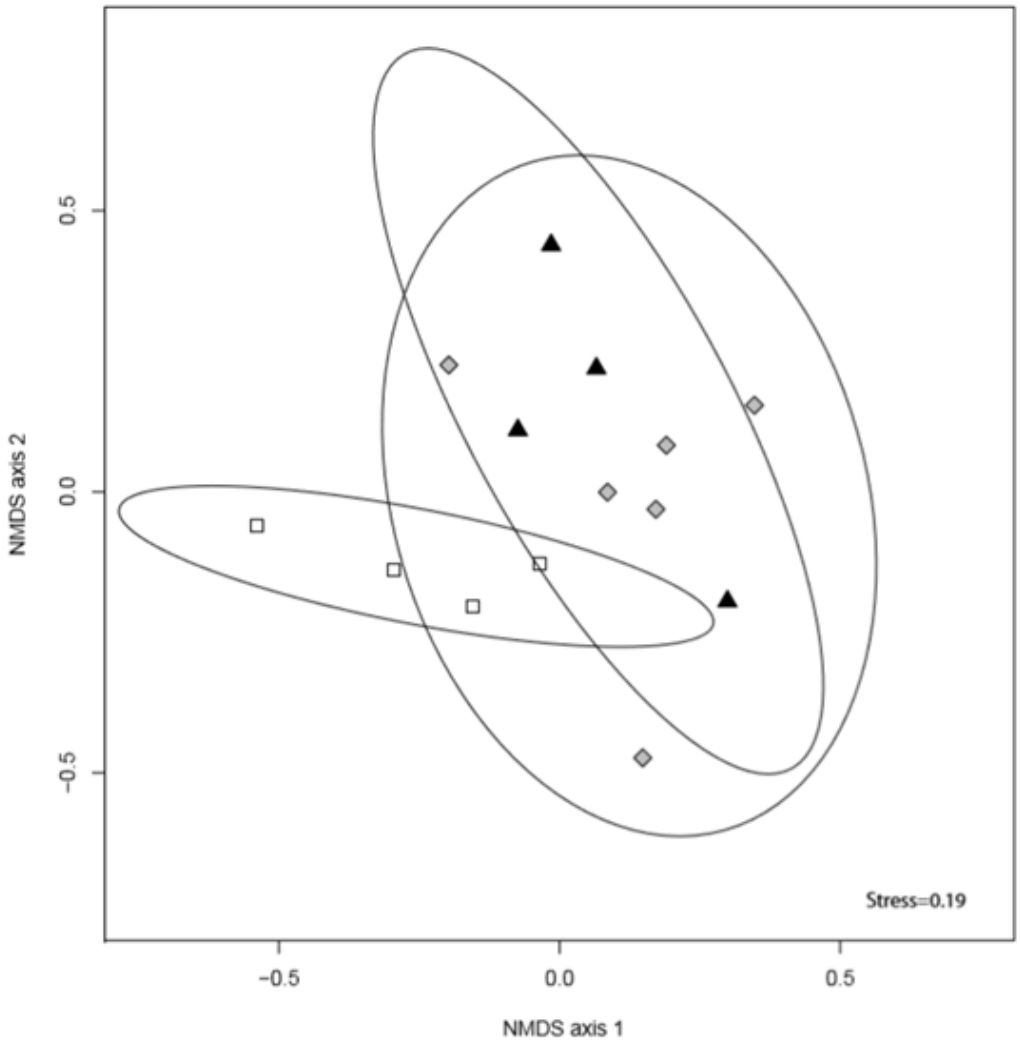

Figure 2-7 Nonmetric multidimensional scaling of Collembola communities in 2015 exposed to nitrogen deposition in Tirasse, Quebec

Data points represent communities for each soil sample. Hollow squares, grey diamonds and black triangles correspond to $N_{control}$, N_{5x}, and N_{10x} treatments respectively. The ellipses are 95% confidence intervals.

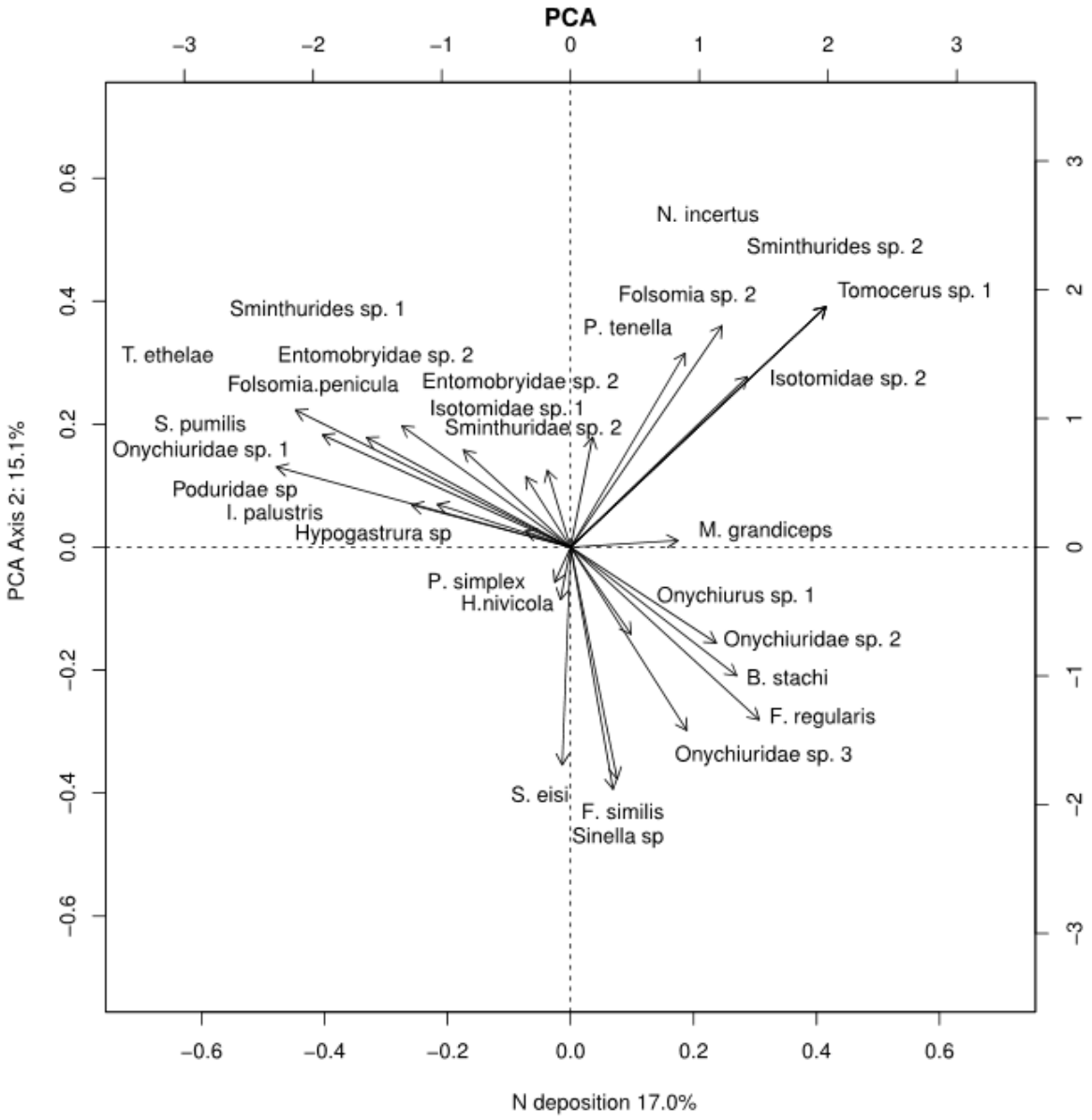

Figure 2-8 Principal component analysis for Collembola communities under nitrogen deposition in 2015 in Tirasse, Quebec

Biplot of the first and second principal component axes with percent variance explained. Positive PCA axis 1 loadings are associated with N_{5x} and N_{10x} treatments whereas negative PCA axis 1 loadings are associated with $N_{control}$ conditions. PCA axis 2 loadings are not associated with any treatment.

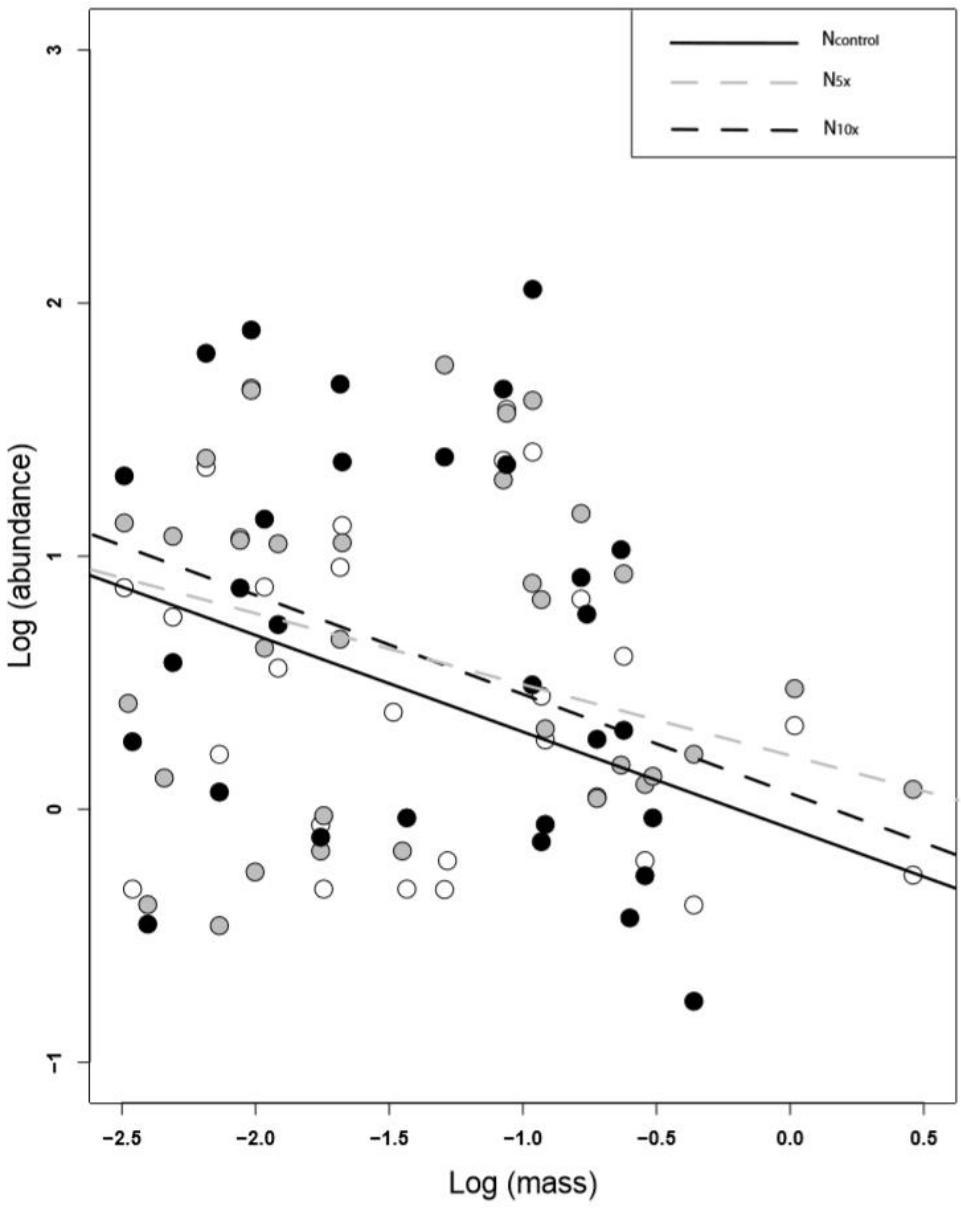

Figure 2-9 Body size spectra of Collembola communities exposed to nitrogen deposition in Tirasse, Quebec

Log transformed Collembola species mass (μg) and standardised abundance (# individuals / 10 g dwt) for temperature treatment relationship across all sampling years in the Tirasse site. White circles with solid lines, and grey and black dots with thatched lines represent $N_{control}$, N_{5x} and N_{10x} treatment species abundances and body size spectra slopes respectively.

2.4 Discussion

2.4.1 Outcomes of ecological stressors are dissimilar

Warming and N deposition are ecological stressors for soil communities (Guo-Liang *et al.* 2009; Bokhorst *et al.* 2012; Siepel *et al.* 2018), through direct and indirect mechanisms. For instance, warming can directly affect soil communities by increasing metabolic costs for soil organisms (Linton *et al.* 1998; Vucic-Pestic *et al.* 2011; Ohlberger & Fox 2013) or can indirectly alter soil environmental conditions such as soil moisture (Samaniego *et al.* 2018). Species can be differentially affected based on their body size with respect to increased metabolic costs (Jucevica & Melecis 2006; Holmstrup *et al.* 2018) that can favour deeper soil-dwelling (euedaphic) soil fauna versus surface dwelling (epigeic) species (Holmstrup *et al.* 2018), and parthenogenetic reproductive strategies (Lindo 2015). In the case of N deposition, mostly indirect effects on the soil communities are associated with decreases in moss cover and increases in vascular plant cover (Bubier *et al.* 2007), altering soil moisture and shifting the abundance of epigeic species (Coulson *et al.* 2003), or excess nutrients can increase microbial biomass, creating favourable conditions for smaller bodied Collembola with faster generation times (Chahartaghi *et al.* 2009).

2.4.2 Warming impacts on Collembola communities

I found only minor changes in the diversity (namely Shannon's and Pielou's index, but not richness or abundance) of Collembola communities exposed to active soil warming over three years, and subtle shifts in community composition. Specifically, I observed more heterogeneous communities composed of a greater proportion of small bodied species, a trend which has been observed in other soil fauna communities (Blankinship *et al.* 2011; Lindo 2015; O'Gorman *et al.* 2017). Shifts in body size spectra is one factor that likely contributed to observed shifts of community composition in my study.

Metabolic costs, particularly for large-bodied organisms, can increase under warming across multiple taxonomic groups (Linton *et al.* 1998; Vucic-Pestic *et al.* 2011; Ohlberger & Fox 2013). From the results of my study, size ranges in Collembola may not be significant enough to see noticeable shifts away from larger body sized species due to

increased metabolic costs. However minor increases in small-bodied, possibly parthenogenetic species, was observed, which is consistent with experimental studies of oribatid mite communities under warming (Lindo 2015). However, the reverse has been observed in the context of warming experiments which examine overwintering. Bokhorst *et al.* (2012) found changes in the body size spectra due to a loss of smaller euedaphic Collembola overwintering in soils warmed with heating cables in a sub-Arctic dwarf shrub heathland. Despite a similar experimental design with Bokhorst *et al.* (2012), I saw an increase in smaller bodied Collembola with little changes in larger bodied Collembola. This suggests that impacts or recovery from overwintering effects on Collembola communities in boreal systems could be minor or rapid, respectively. One possibility is that high snow cover in the boreal region of central Quebec maintained soil moisture conditions under warming treatments. Strong relationships between soil moisture and Collembola abundance are well known (Krab *et al.* 2010; Kardol *et al.* 2011), and it is by this mechanism through which Collembola abundance can be affected. Soil moisture did not decrease in warming treatments in this experiment, such that changes in habitat quality affecting abundance likely did not occur.

Shifts in community structure to smaller body sized, primarily euedaphic Collembola may be the result of changes in microbial communities under warming (Asemaninejad *et al.* 2018). Euedaphic and epigeic Collembola occupy two distinct areas within the soil profile, where euedaphic Collembola generally consume mycorrhizal fungi, while edaphic Collembola consume saprotrophic fungi (Siddiky *et al.* 2012, Anslan *et al.* 2018). Asemaninejad *et al.* (2018) found warming favoured mycorrhizal fungi, but this effect was mostly due to shifts in aboveground plant community composition. However, cascading trophic effects onto fungal-feeding soil organisms such as Collembola are possible.

2.4.3 The effect of N deposition on Collembola communities

Collembola abundance, richness, diversity and community composition show little change in response to increases in N deposition in this study despite the long-term (*i.e.*, chronic) nature of the deposition treatments. Other research has also shown little effect of N deposition or enrichment on Collembola (Rzeszowski *et al.* 2017), despite altered

vegetation cover (Bokhorst *et al.* 2014), microbial biomass (Johnson *et al.* 1998) or pH (Ochoa-Hueso *et al.* 2014), all of which are key factors in structuring soil communities. Ochoa-Hueso *et al.* (2014) showed that N deposition in a semi-arid system had a beneficial effect on Collembola abundance at 3× natural deposition rates, but caused a decrease at 9× rates, further increases in N inputs decreased abundance. This was proposed to occur due to increased soil acidification and increases the dominance of ammonium within the soil.

Species in my study associated with $N_{control}$ conditions were *I. palustris*, *Hypogastrura* sp., and Onychiuridae sp. 3, while the main species related to N deposition treatments was *M. grandiceps*. *Metisotoma grandiceps* is a Holarctic species and is one of only a few Collembola species considered predatory; this species, while variable in size, is typically > 1 mm (Potapov *et al.* 2018). As a result, I noted minor shifts in the body size spectra for Collembola communities exposed to increased N deposition with an increase in all size classes (N_{10x}) or larger species (N_{5x}). Changes in body size are previously observed, but contrary to the findings of this study body sizes have been shown to decrease with nutrient additions (Mulder & Esler 2009; Turnbull 2014), which suggests that the directionality of N deposition effects on body size may be related to changes in vegetation, other soil faunal groups, or altered microbial communities.

2.4.4 Implications of ecological stressor impacts on Collembola and the boreal forest

Experimental treatments in both the Simoncouche and Tirasse experiments were designed to emulate climate shifts and anthropogenic inputs of nutrients predicted for the boreal forest region in the next 50-100 years (Hansen *et al.* 1995; Galloway *et al.* 2004). However, in addition to warming and increased N deposition there will be other co-occurring environmental changes. For instance, precipitation events are expected to become less frequent but more severe (IPCC 2013), and I would predict Collembola communities to experience shifts in abundance and composition under drought (Pflug & Wolters 2001; Guo-Liang *et al.* 2009), and under heavy precipitation and flooding (Turnbull & Lindo 2015). Furthermore, warmer temperatures and drier soil conditions will increase the incident of fire in forest systems, which will also directly affect soil

nutrients and vegetation cover (Gabysheva & Isaev 2015), soil moisture (Macdonald & Huffman 2004), and impact Collembola communities, especially epigeic species (Huebner *et al.* 2012; Malmström 2012). Recovery of Collembola communities post fire disturbance can be rapid (3-5 years) or long-term (20-50 years) depending on the severity of the fire (Huebner *et al.* 2012), forest type and post-disturbance plant succession (Malmström 2012). Finally, boreal forests are also expected to experience longer growing seasons due to climate change (Brinkmann 1979), which can increase yearly collembolan activity through population fluctuations (Anslan *et al.* 2018), shifts in rates of movement and in the case of euedaphic Collembola, shifts in foraging soil horizon (Boiteau & Mackinley 2012). Increased Collembola grazing may have cascading effects on the microbial component of the soil food web and therefore decomposition processes and nutrient cycling (Caravaca & Ruess 2014).

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Chapter 3

3 Top-down and bottom-up control on Collembola community structure is mediated by warming

3.1 Introduction

3.1.1 Impacts on top-down and bottom-up effects on communities

Shifts in predators and/or basal resources can elicit changes in mid-trophic level species through top-down and bottom-up control, respectively. Bottom-up control has historically been considered as the main process that structures detrital communities (Polis & Strong 1996) due to the donor control nature of detritus. However, recent literature on soil food webs suggests that top-down, rather than bottom-up, control is equally or more important in structuring soil communities (Lenoir *et al.* 2007; Schneider & Maraun 2009), suggesting a need to incorporate both top-down and bottom-up processes in our understanding of soil food webs (Buchkowski 2016).

The direct and indirect effects of top-down control on prey community structure are well studied in aboveground terrestrial and aquatic systems (Elmhagen & Rushton 2007; Lemmens *et al.* 2018) yet are relatively unexplored in soil systems (but see Fraser & Grime 1998; Crowther *et al.* 2013). Studies in non-soil systems demonstrate that shifts in predation efficiency (Lunt & Smee 2015), prey susceptibility (Hammill *et al.* 2017), or the introduction of new or invasive predators (Wilson & Driscoll 2017), can increase the strength of top-down control on prey communities (Wesner *et al.* 2012). The direct effects of increased top-down control can result in an overall reduction in prey biomass and diversity (Katano *et al.* 2015), or changes in prey species composition (McQueen *et al.* 1989), prey size (Nurminen *et al.* 2017) or both (Sinclair *et al.* 2003) due to predator preferences in prey species. More basally, feeding rates and community composition of mid-trophic level soil species, such as Collembola (springtails), can shift microbial

community structure (Crowther *et al.* 2013), through feeding selection preferences (Chahartaghi *et al.* 2005).

Increases in nutrient availability commonly induce beneficial bottom-up effects on soil microbes (Hines *et al.* 2006; Bradford *et al.* 2008) that can cascade to increase Collembola abundance (Hägvar & Klanderud 2009), that can lead to changes in the relative abundance and dominance of Collembola species (Fountain *et al.* 2008). That said, long-term nitrogen deposition can negatively affect Collembola abundance and richness (Xu *et al.* 2009), and the effect observed may vary depending on the level of soil nutrient addition (Ochoa-Hueso *et al.* 2014). Therefore, while nutrient addition can act as a bottom-up effect that enhances microbial resources available for mid-trophic level groups, there is a point these additions cause negative effects on abundance and richness.

3.1.2 Warming as a bottom-up effect and interactive component in regulating top-down and bottom-up control

Warming may act as an ecosystem 'enrichment' parameter to create bottom-up effects. For instance, warming often increases net primary productivity through enhanced growth rates, subsequently increasing resources available for consumers (Krumhardt *et al.* 2016). In soil systems warming tends to increase microbial activity, leading to greater microbial biomass and shifting composition (DeAngelis *et al.* 2015) from fungal-dominated to bacterial-dominated communities (Frey *et al.* 2008). These changes may cascade to impact Collembolan community structure. Brose *et al.* (2012) suggests that increased temperatures may also have direct effects on soil microarthropod communities through increased metabolic rates, particularly for small-bodied species. Lindo (2015) demonstrated that warming drove compositional shifts in belowground fauna communities due to the increased abundance of small-bodied species. At the same time, warming increases the metabolic costs for organisms (Brown *et al.* 2004; Brose *et al.* 2012), and are greater for larger body sized organisms in a higher trophic position (i.e. predators). Yet Lang *et al.* (2014) also found that warming can increase predation pressure from predatory mites on Collembola communities. As such, warming may impact the relative strength of top-down and bottom-up control in ecosystems.

Top-down and bottom-up effects are relatively well-studied in isolation, but these processes can act simultaneously to affect ecological communities. Similarly, warming effects as enrichment scenarios have been demonstrated in numerous systems, yet top-down and bottom-up effect interactions are rarely studied (but see Meserve *et al.* 2003 and Lynam *et al.* 2017). This is despite both processes occurring simultaneously within natural systems, and few studies have explored the effects of top-down and bottom-up control mediated by warming (but see Kratina *et al.* 2012; Shurin *et al.* 2012; Velthuis *et al.* 2017). Interaction effects between warming, bottom-up and top-down control could give important insight into community level responses to multiple abiotic shifts.

3.1.3 Objectives and predictions

The objective of my research was to assess changes in Collembola community (richness, abundance, and composition) due to top-down predation and bottom-up nutrient enrichment under two temperature treatments in an experimental soil mesocosm system. I hypothesize that Collembola richness, abundance, and community composition will be affected by increased predation pressure and nutrient enrichment through top-down and bottom-up processes. However, I also hypothesize that warming will weaken top-down while strengthening bottom-up controls on Collembola communities. Overall, the interactive effects of simultaneous top-down and bottom-up effects under warming will lead to the relatively stronger bottom-up effects of temperature and nutrient addition treatments compared to increases in predation pressure.

3.2 Materials & methods

3.2.1 Soil collection, homogenization and characterization

Highly organic forest floor soil was collected from the top litter and fragmentation layer (0-10 cm) in a fir-dominated coniferous forest from Denman Island, British Columbia in September 2016. This soil was transported to and stored at Western University in

London, Ontario in Rubbermaid® bins for storage at 4°C. Forest floor soil from a second fir forest site sampled in 2013, found not to contain fauna and had low microbial activity, were used to increase the volume of total soil used in the experiment. Soils were homogenized, and the following preliminary chemical and biological variables were measured: soil moisture content, pH and electrical conductivity, available nitrogen and phosphorus, microbial activity and biomass, Collembola richness and abundance, and predator density.

Percent moisture content was determined by using five 5 g subsamples of soil dried at 60°C for 48 hrs and calculated gravimetrically using the following equation:

$$\text{Moisture content (\%)} = ((\text{wet weight (g)} - \text{dry weight (g)}) / \text{wet weight (g)}) \times 100.$$

Electrical conductivity and pH were measured using a 1:2 slurry of 10 g soil with 20 ml water stirred and settled for 1 h. The pH of the soil slurry was measured using a digital reader with a glass electrode, and electrical conductivity was measured following vacuum filtering using a digital conductivity meter probe. Nitrogen (NH_4^+, NO_3^-) and phosphorus (PO_4^+) availability was assessed using 5 g dry weight equivalent soil, shaken for 1 h in either 40 ml of 2N potassium chloride or Bray's extract (dilute ammonium fluoride), respectively. Extracts were run using the indophenol blue method (NH_4^+), hydrazine method (NO_3^-) and the fluoride method (PO_4^+) on a continuous flow nutrient auto-analyser. Microbial activity was measured as heterotrophic respiration (CO_2 flux) on a Licor Infrared Gas Analyser (IRGA) over 4 hrs; microbial biomass was determined from the same samples using the direct chloroform extraction method outlined in (Vance *et al.* 1987).

The initial Collembola community was characterised from six replicates of approximately 40 g each, extracted using the Tullgren funnel method where a heat and desiccation gradient actively drives microarthropods downward into a 75% ethanol preservative over 72 hrs. Extracted Collembola were enumerated and identified to species level, where possible, using a key of Collembola in North America (Christiansen & Bellinger 1984) and standardised per 10 g dry weight. Total predator density was calculated as the total number of mesostigmatid mites (Acari: Mesostigmata) per 10 g dry weight.

3.2.2 Experimental design

Approximately 120 g wet weight of soil was placed in 80 experimental mesocosms constructed from 500 ml glass mason jars with vented lids allowing for approximately 50 ml headspace. Each mesocosm was fitted with a 5 cm Rhizon® sampler to collect and filter soil porewater biweekly. Mesocosms were designated to three different treatments each with two levels in a full factorial design to include all interactions with five replicates per treatment. Treatments were: incubation temperature (12°C, 16°C), nutrient addition (no addition ($N_{control}$), enriched with nutrient solution (N_{add})), and predator loading (no predators added ($P_{control}$), double the predator density (P_{add})). The 12°C temperature treatment was chosen as an ambient temperature (control) as it is the average temperature of the boreal forest during the growing season, while 16°C was chosen as a warming treatment based on climate change projections of +4°C within the next century (IPCC 2013). Temperatures were maintained using environmental growth chambers under dark conditions. Nutrient addition treatments were performed biweekly using a nutrient solution of 0.209 g potassium phosphate, 0.1783 g ammonium nitrate and 0.01 g micronutrients (Zn, Ca) in 1.2 L of distilled water. These values are adapted from a nutrient addition experiment performed by Basiliko *et al.* (2006).

Mesocosm moisture content was maintained gravimetrically by adding deionised H_2O and/or nutrient solution added equal to the weight lost during the week (~ 2 ml) by recording the total weight of each mesocosms including the soil and jar weight. Soil predators were a commercial biocontrol agent (Mesostigmata: *Stratiolaelaps scimitus*) selected based on preferred prey size and known thermal tolerances. Fifteen soil predators were added initially to the predator addition mesocosms, with an additional five predators added biweekly for the duration of the experiment. The experiment was fully replicated for destructive sampling after 3 and 6 months (2 temperature × 2 predator × 2 nutrients treatments × 5 replicates × 2 sample times = 80 mesocosms total).

3.2.3 Destructive sampling

Half the mesocosms (N=40) were destructively sampled after three months, and the remaining mesocosms (N=40) after six months for Collembola communities (richness,

abundance, composition, and body size). Collembola were extracted from approximately 40 g of soil using the Tullgren funnel method as described above. Extracted Collembola were identified and enumerated at the species level where possible, and predators were enumerated. Collembola richness and abundance were standardized by 10 g dry weight of soil.

3.2.4 Data analysis

Collembola diversity was calculated using Shannon's diversity (H') and Pielou's evenness (J) for each treatment using the {vegan} package in R (version 3.1.2; R Development Core Team). Total standardised Collembola abundance and richness, Shannon's diversity and Pielou's evenness were evaluated using factorial ANOVA at each time point separately. The Collembola community composition was analysed using Bray-Curtis measures of dissimilarity for standardised abundances of Collembola species with a Hellinger transformation. Collembola community composition was visualised using non-metric multidimensional scaling (NMDS) in R using the {metaMDS} function, and the significance of dissimilarity for main treatment effects was performed with permutational ANOVA (PERMANOVA) using the {adonis} function in R. For the NMDS, the final ordination presents dissimilarities in species composition between samples; data points plotted further away from each other represent samples that are more dissimilar than data points that plot closer together. Heterogeneity (i.e. variability among mesocosm composition) was quantitatively evaluated using the similarity percentage (SIMPER) package in PRIMER 5 (PRIMER-E Ltd., 2001), which also identifies species that contribute to similarity/dissimilarity among treatments. Hellinger transformed community data were also used in a Principal Components Analysis (PCA) to examine which species were driving compositional trends. Subsequent main factor ANOVA was used on sample factor scores from the PCA to determine whether treatments were significantly related to Collembola composition.

3.3 Results

3.3.1 Collembola richness, diversity, and abundance trends across treatments

A total of 1810 individual Collembola from 23 species were collected from the initial characterisation phase (T_0), three months after the start of the experiment (T_3) and after six months experimental treatment (T_6) (Appendix 3.1). The average Collembola abundance and species richness at the start of the experiment was 11.4 individuals (±0.9) and 5.2 species (±0.7 SE) per 10 g dwt, respectively (see Appendix 3.1). The average Collembola abundance and species richness after three months was 16.9 (±1.8) individuals and 5.9 species (±0.5), and at six months were 18.7 (±2.6) individuals and 4.5 species (±0.3) per 10 g dwt, respectively.

After three months (T_3) predator addition treatments had significantly greater collembolan species richness ($F_{1,32}$=11.52, p=0.002), while nutrient addition had a marginally negative effect ($F_{1,32}$=4.00, p=0.054), and all treatments combined had a significant interaction ($F_{1,32}$=11.42, p=0.002). Species richness was greatest under ambient temperatures and no nutrient addition when predators were added, and lowest in the warming, nutrient addition, and no predator addition treatment (Figure 3.1A). Similar treatment effects were observed for Shannon's diversity (T_3: predators: $F_{1,32}$=14.78, p=0.001; three-way interaction: $F_{1,32}$=7.83, p=0.009), while evenness was significantly increased under predator addition (T_3: predators: $F_{1,32}$=11.81, p=0.002). After three months, Collembola abundance was reduced under nutrient addition and warming when predators were not present compared to warmed conditions without nutrients and predators (Figure 3.1B). There were no significant main treatment effects altering Collembola abundances at T_3 or T_6, yet the abundance of Collembola in mesocosms displayed a significant three-way interaction at T_3 ($F_{1,32}$=6.92, p=0.013) and a significant two-way interaction between temperature and predator treatments ($F_{1,32}$=7.85, p=0.009) at T_6. After six months (T_6) warming significantly decreased collembolan species richness ($F_{1,32}$=8.28, p=0.007) (Figure 3.2A), while predator addition increased Collembola abundance at 12°C, but decreased Collembola abundance at 16°C, decreased with predator addition (Figure 3.2B). Shannon's diversity also decreased under warming

($F_{1,32}$=10.70, p=0.003), but increased under predator addition ($F_{1,32}$=6.42, p=0.016). Evenness values also decreased under warming and marginally increased in predator addition treatments at T_6 (T_6: warming: $F_{1,32}$=13.11, p=0.001, predators: $F_{1,32}$=3.89, p=0.057) (Table 3.1).

3.3.2 Collembola community composition after three and six months

Nutrient addition did not contribute as a main factor to structuring Collembola communities (T_3: $F_{1,38}$=1.80 p=0.096; T_6: $F_{1,38}$=1.05 p=0.401). However, predator addition treatments were significant in structuring Collembola communities after three months (predators: $F_{1,38}$=2.77 p=0.004; warming: $F_{1,38}$=2.40, p=0.049), while warming significantly structured communities at T_6 (warming: $F_{1,38}$=6.18, p<0.001). After three months, the collembolan communities under predator addition treatments (P_{add}) showed a distinct pattern of homogenisation (Figure 3.3A), whereby predator addition at both temperatures led to communities that are more similar to each other (and cluster more closely in ordination space) than $P_{control}$ mesocosms. This homogenisation under predator addition treatment was still observed after six months, but only under control temperature treatments, while overall, warming treatments shifted the Collembola community after six months (Figure 3.3B).

Communities under warming became more dissimilar over time where average dissimilarity between treatments was 70.0% and 76.3% at three and six months respectively. The small-bodied species Onychiuridae sp. 1 contributed to both the average similarity within warming (16°C) treatments (35.6% contribution) and the dissimilarity (13.8%) between temperature treatments after three months, while two larger bodied species (*Willemia* sp. 1 and *Acherontiella sabina* Bonet, 1945) contributed the most to the similarity of the communities at ambient (12°C) temperature (38.0% combined contribution). After six months experimental treatment, the small-bodied species such as *Neelides dianae* (Christiansen & Bellinger, 1981) contributed most to the similarity within warming treatments (38.2%), with *Willemia* sp. 1 continuing to contribute most to the similarity under 12°C treatments (24.4%).

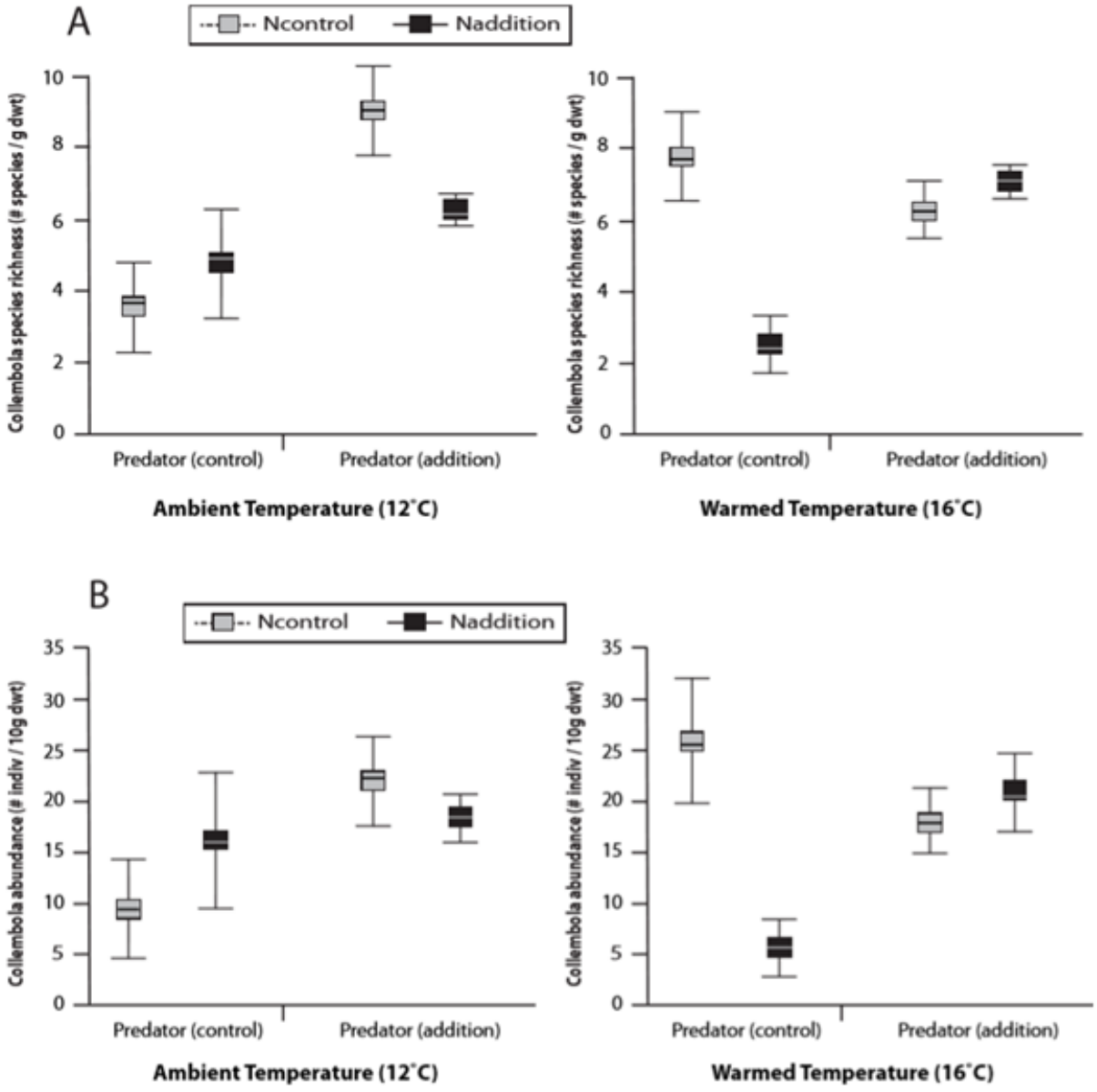

Figure 3-1 Standardised values for Collembola A) species richness (# species / g dwt) and B) abundance (# individuals / 10 g dwt) after three months of experimental treatment in soil mesocosms

Boxes are standard errors with means as black and white lines. Treatment denoted N_{contol} refers to mesocosms with no nutrient solution added, while $N_{addition}$ refers to mesocosms where nutrient solution was added bi-weekly.

Table 3-1 Collembola diversity and evenness in soil mesocosms exposed to experimental treatments of warming, nutrient addition and predator addition

	Three months (T_3)			
	$P_{control}$		$P_{addition}$	
Diversity	N_{cont}	N_{add}	N_{cont}	N_{add}
12°C	1.03 (0.32)	1.34 (0.39)	2.10 (0.11)	1.81 (0.11)
16°C	1.95 (0.10)	0.92 (0.27)	1.81 (0.26)	1.90 (0.04)
	Six months (T_6)			
	$P_{control}$		$P_{addition}$	
Diversity	N_{cont}	N_{add}	N_{cont}	N_{add}
12°C	1.52 (0.20)	1.43 (0.17)	1.80 (0.11)	1.72 (0.26)
16°C	1.24 (0.18)	0.88 (0.07)	1.59 (0.16)	1.19 (0.17)
	Three months (T_3)			
	$P_{control}$		$P_{addition}$	
Evenness	N_{cont}	N_{add}	N_{cont}	N_{add}
12°C	0.33 (0.10)	0.43 (0.12)	0.67 (0.03)	0.58 (0.03)
16°C	0.63 (0.03)	0.30 (0.09)	0.57 (0.04)	0.56 (0.04)
	Six months (T_6)			
	$P_{control}$		$P_{addition}$	
Evenness	N_{cont}	N_{add}	N_{cont}	N_{add}
12°C	0.49 (0.06)	0.46 (0.06)	0.55 (0.04)	0.55 (0.08)
16°C	0.39 (0.05)	0.28 (0.02)	0.45 (0.04)	0.38 (0.06)

Shannon diversity and Pielou's evenness of Collembola communities following three (T_3) and six months (T_6) experimental treatment. Values are means with standard error in parentheses.

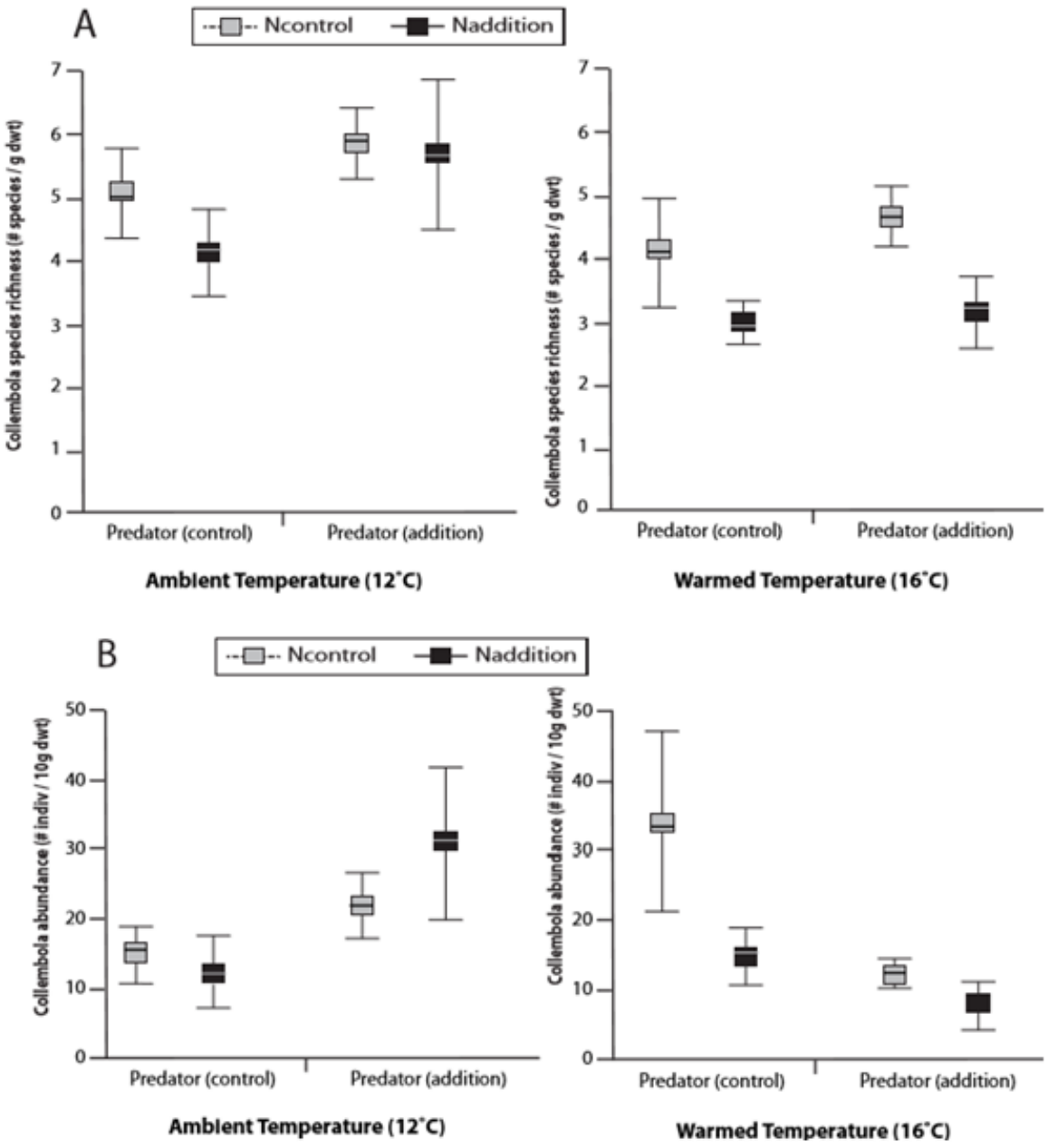

Figure 3-2 Standardised values for Collembola A) species richness (# species / g dwt) and B) abundance (# individuals / 10 g dwt) after six months of experimental treatment in soil mesocosms

Boxes represent standard errors with means as black and white lines. Treatment denoted N_{contol} refers to mesocosms with no nutrient solution added, while $N_{addition}$ refers to mesocosms where nutrient solution was added bi-weekly.

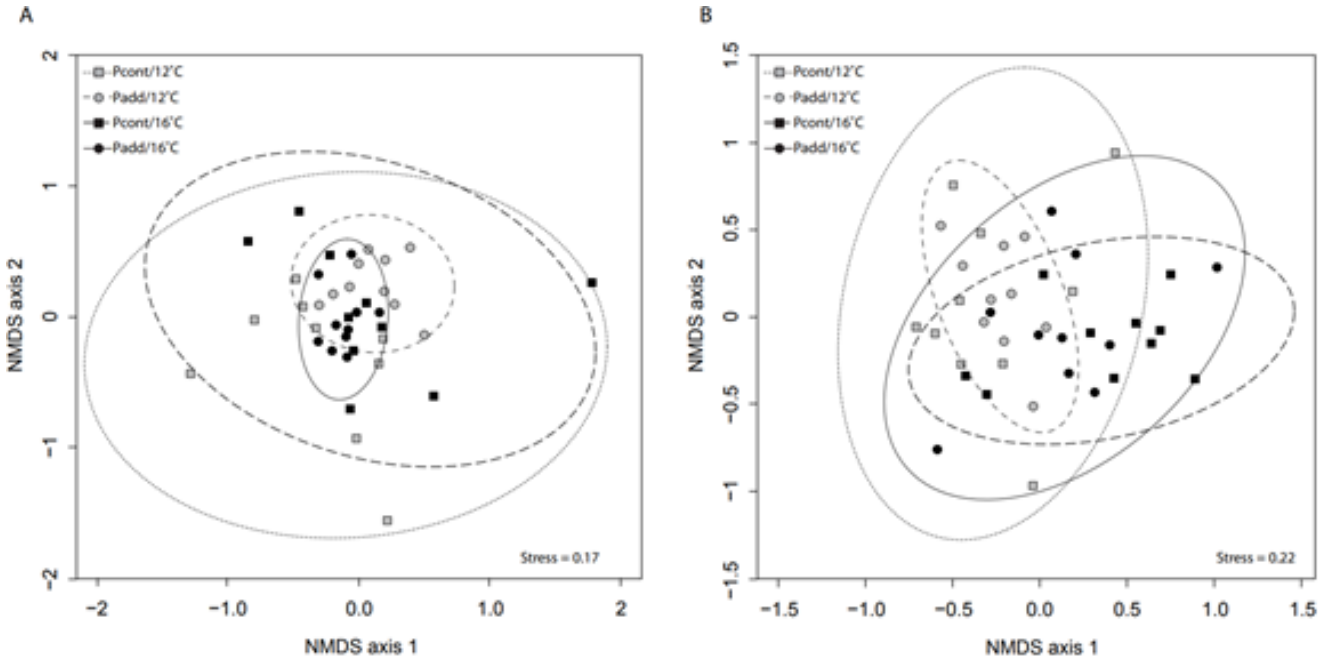

Figure 3-3 Nonmetric multi-dimensional scaling (NMDS) ordination biplots for Collembola community composition showing predator addition and warming treatment crosses in soil mesocosms

Panel A) shows communities at three months and B) at six months of experimental treatment. Data points represent communities for individual mesocosms. Grey squares are communities under 12°C and $P_{control}$ treatment combinations, grey circles are communities under 12°C and $P_{addition}$ treatments, black squares are communities under 16°C and $P_{control}$ treatment combinations, and black circles are communities under 16°C and $P_{addition}$ treatments. The ellipses are 95% confidence intervals.

Communities under predator treatments also became more dissimilar over time where average dissimilarity between predator treatments was 70.0% and 74.2% at three and six months respectively. Under predator addition treatments after three months communities were 45% similar compared to $P_{control}$ treatments that were only 23% similar. *Willemia* sp. 1 contributed the most both to average similarity within predator addition treatments (21.9% contribution) and the dissimilarity (15.6%) between predator treatments. Onychiuridae sp. 1 and *Willemia* sp. 2, both small-bodied species, contributed most to the similarity under $P_{control}$ treatments (39.2% combined contribution). After six months, *Willemia* sp. 1 and *N. dianae* contributed most to the similarity within $P_{control}$ treatments (46.8% combined contribution), with large-bodied *Willemia* sp. 1 contributing most to the similarity under predator addition treatments (26.0%).

The PCA of the Collembola community after three months suggests all factors structured community composition, with PC axis 1 explaining 16.3% of the variation, while the second PC axis (PC2) explained an additional 10.3% of the variation (Figure 3.4A). Site scores for PC axis 1 were significantly related to main effects of warming and nutrients (warming: $F_{1,38}$=4.31, p=0.045, nutrients: $F_{1,38}$=4.28, p=0.045) with Poduridae sp. 2, Poduridae sp. 3, *Tomocerus* sp. and Onychuridae sp. 3 having high positive scores relating to ambient temperature (12°C) and nutrient ($N_{control}$) conditions. Site scores for the second PC axis were marginally related to the main effect of predator treatments (predators: $F_{1,38}$=3.04, p=0.089) with *Dagamaea tenuis* (Folsom, 1934), Poduridae sp. 2, and Poduridae sp. 3 related to predator additions, while *Willemia* sp. 2, *Folsomia* sp. 2, and Entomobryidae sp. were negatively related to predator additions.

After six months of experimental treatment, the Collembola community was structured by temperature treatments with PC axis 1 and PC axis 2 explaining 17.0% and 14.7% of the variation in the community composition, respectively (Figure 3.4B). Site scores for PC axis 1 were significantly related to warming (PC1, $F_{1, 38}$= 22.61, p=0.01) with *Folsomia fimetaris* (Linneus 1785), *Micranurophorus musci* Bernard 1977, and *Folsomia* sp. 1) having high positive scores under 12°C temperatures and only *N. dianae* having high negative scores under warming conditions. Site scores for PC axis 2 were not significantly related to any experimental treatment.

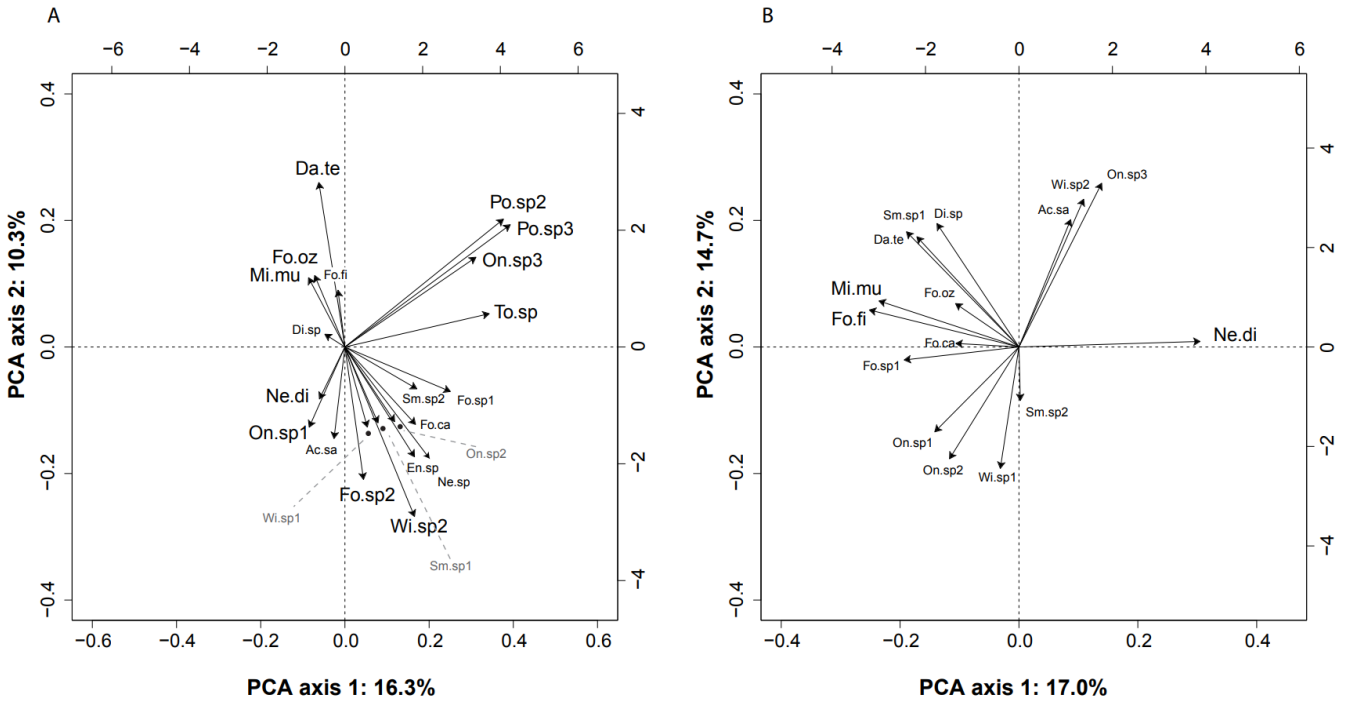

Figure 3-4 Principal component analysis for Collembola communities in soil mesocosms after A) three months and B) six months experimental treatment

Biplot of the first and second principal component axes with percent variance explained. At three months, positive PCA axis 1 loadings are associated with $N_{control}$ and 12°C treatments, while negative axis 1 loadings are associated with N_{add} and 16°C treatments. Predator addition was associated with positive values on PCA axis 2, while negative values were associated with $P_{control}$ treatments. At six months, temperature was associated with PCA axis 1, where positive values were associated with 12°C treatments and negative with 16°C treatments.

3.4 Discussion

3.4.1 Warming mediates top-down and interactive effects

Predator addition and warming treatments caused shifts in Collembola abundance interactively and community composition independently, suggesting that warming enhances the effects of top-down control on soil organisms. Shurin *et al.* (2012) also found interactive effects of warming and predators in an experimental system of aquatic mesocosms (cattle tanks) using planktivorous fish to induce top-down control and nutrient loading (eutrophication) to induce bottom-up effects. The authors found that warming enhanced top-down control on zooplankton with cascading effects on periphyton, phytoplankton and bacteria. While I found similar results of warming enhanced top-down control, I found no evidence that nutrient addition acted as a bottom-up effect for soil organisms.

There is growing evidence for top-down effects being critical in food web shifts (Schmitz 2007; Lynam *et al.* 2017). Predator addition treatments resulted in homogenized collembolan communities under ambient and warmed conditions, but changes in abundance and richness were dependent on temperature treatment. Changes in predator activity (Lemoine *et al.* 2017), metabolic efficiency, or behavior (Jolly *et al.* 2016) could have arisen under warming. For instance, larger bodied predators have greater metabolic costs under warming than their small-bodied prey, which could have increased predation rates on Collembola. Our soil predator *Stratiolaelaps scimitus*, is a generalist predator with a wide temperature tolerance (15-25°C) and can consume 5-10 prey items per day (Cabrera *et al.* 2005). The homogenization of the Collembola community under increased predation appears related to prey preferences or availability as small-bodied prey were more likely to decrease under increased predation. For instance, *A. sabina* the largest species in the study, did not experience declines in abundance with predator treatments, suggesting that it may have been too large a prey item to capture for the introduced predator. Additionally, I found that predator addition structured Collembola communities with several species associated with predator additions (*D. tenuis*, Poduridae sp. 2, Poduridae sp. 3), and several species negatively related to predator additions (*Willemia* sp. 2, *Folsomia* sp. 2, Entomobryidae sp.).

Warming in this study also increased small-bodied Collembola. Body size is increasingly regarded as an important estimate of response in soil systems (Petchey & Belgrano 2010) that can change under warming through 'community downsizing' (i.e. increases in smaller-bodied species) in soil communities (Lindo 2015). Other studies have also observed specific Collembola species prefer warmed conditions (Yan *et al.* 2015) along with trends of soil animals having smaller body sizes (Brose *et al.* 2012; Reuman *et al.* 2014). Shifts in body sizes can cause changes in energy transfer (Yvon-Durocher *et al.* 2011; Ersoy *et al.* 2017) and functional diversity (Rudolf *et al.* 2014), making body size shifts a key response variable in understanding both shifts in food web structure and ecosystem function. Under warming treatments, smaller bodied Collembola, such as members of the Onychiuridae family, drove greater similarity while similarly, the smallest species, *N. dianae* dominated community structure.

3.4.2 Nutrient effects on Collembola abundance and community structure

I found little evidence for bottom-up control in my experimental soil system, as there was no direct effect of nutrient addition on microbial biomass, Collembola abundance, or Collembola community structure. This suggests that either, the system was not nutrient limited, or that the system was limited by another micronutrient not added. Nitrogen and phosphorous compounds are both important nutrients in soil systems, however, there is some suggestion that phosphorous is a larger contributor to structuring soil collembolan communities than nitrogen (Rzeszowski *et al.* 2017). The nutrient addition treatment for this study was modified from Basiliko *et al.* (2006), who found nutrient enrichment had a strong bottom-up effect on microbial biomass in peat. Boreal forest soils are often N limited, but perhaps differences in soil pH, moisture content, or the microbial communities themselves, required greater nutrient inputs to induce a bottom-up effect. Interestingly, temperature also had no direct effect on microbial biomass, even though it is known to promote and accelerate microbial growth up to a thermal optimum (DeAngelis *et al.* 2015). That said, nutrient addition played a key role in altering collembolan communities in the presence of three-way interactive effects. For instance, nutrient addition in combination with predator control treatments and warming greatly

reduced collembolan species richness and abundance. The Collembola species associated with this combination of treatments were smaller bodied Onychiurid and Hypogastrurid species. Hägvar & Klanderud (2009) found that parthenogenic Collembola species are more abundant and dominate communities under nutrient addition and warming. While the reproductive life histories of the species in my study are not confirmed, approximately 10-15% of Onychiurid species are presumed to be parthenogenetic (Chernova *et al.* 2010).

3.5 Conclusion

Current anthropogenic environmental impacts on ecosystems, are multifaceted, globally reaching and act simultaneously. Ecological communities in natural systems are subject to multiple shifts in abiotic factors that can interactively create shifts in community structure within soil communities. Globally, temperatures are predicted to rise 4°C by 2100 in climate change scenarios (IPCC 2013), nutrient loading has increased available nitrogen twofold and phosphorous threefold (Galloway *et al.* 2004) and introduced invasive species have already and continue to alter communities in the new ecosystems they invade (Coyle *et al.* 2017). Research has shown both abiotic and biotic regime shifts to interactively alter community dynamics in terrestrial and aquatic systems. Recent research aims to examine these interactive effects in soils (see Coyle *et al.* 2017) and my results now show shifts in soil collembolan communities. My research also stresses the different outcomes between independent and interactive effects. This study aimed to replicate the complex shifts transforming soil ecosystems due to anthropogenic change and has shown that soil collembolan communities are not immune to these effects. Examining top-down and bottom-up processes and especially their mediation by warming gives important insight into soil community dynamics in the context of global change.

3.6 References

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Chapter 4

4 Environmental impacts on soil organisms

4.1 Future global, regional, and local impacts of anthropogenic change on soil communities

Climate change is projected to greatly affect mid to high latitude regions through increased rates of precipitation and accelerated warming (IPCC 2013). Climate warming can accelerate decomposition where decomposition rates may increase in high latitude regions (Wall *et al.* 2008). Other anthropogenic impacts on soil nutrient availability and introduction of new invasive species occur simultaneously with changes in regional climate. Many studies of soil decomposition and soil fauna communities focus on warming as a single factor that affects communities (Garcia-Pichel *et al.* 2013), despite multiple environmental changes affecting these communities. Multiple sources of ecological stressors or top-down and bottom-up forces may interact to exacerbate change on soil communities. With the high biomass and ubiquity of Collembola across a wide range of ecosystem types (Hopkin 1997), coupled with their sensitivity to environmental change (e.g. Meserve *et al.* 2003 and Lynam *et al.* 2017), they are a group globally vulnerable to ecological stressors. My study evaluated the effects of warming, increases in soil nutrients and increases in predation pressure on Collembola as a mid-trophic group, susceptible to both top-down and bottom-up pressures, both as single factors (Chapter 2) and combined treatment interactions (Chapter 3). In both studies, warming was shown to homogenize or shift community composition through increases in smaller bodied soil dwelling species, which primarily live deeper within the soil horizon (Hopkin 1997).

While my study did not find increases in microbial biomass, other studies have observed increases in biomass under warming especially in colder systems (Chen *et al.* 2015) and nutrient addition (DeAngelis *et al.* 2013). Soil nutrient availability has been observed to increase microbial biomass (Fountain *et al.* 2008) and affected some belowground soil fauna groups such as nematodes (Gough *et al.* 2012). Direct effects on Collembola from increases in soil nutrient reservoirs have been varied, and most research find weak effects

on communities (Ochoa-Hueso *et al.* 2014), or non-effects (Mitchell *et al.* 2016). Collembola communities react strongly to litter quality or habitat diversity (Querner *et al.* 2018), which are described as the main factors driving community change in single crop agriculture systems rather than direct impacts from nutrient pollution (Mitchell *et al.* 2016). While results from Chapter 2 found increased nitrogen deposition rates affect community structure and community body size, it is difficult to determine the reason for this shift. Indirect effects of nutrients on both vegetation cover and microbial abundance may not sufficiently strong enough to induce bottom-up effects, or a habitat fragmentation disturbance effect on Collembola abundances.

4.2 Measures of change in soil ecology

A key result from Chapter 2 were the observed trends in Collembola body size spectra, where smaller bodied organisms became more abundant under warming treatments. My results are similar to findings in other studies (see Holmstrup *et al.* 2012), and with physiological processes within organisms, such as metabolic scaling theory, which postulates that metabolic rates correlate with both temperature and body size (Maino *et al.* 2014). Smaller bodied Collembola are mostly soil dwelling species, which feed upon fungal mycorrhizae rather than larger bodied litter dwelling species that feed on saprotrophic fungi. I also found that nitrogen deposition favoured larger bodied surface dwelling Collembola but only at mid-level treatment of N deposition. This could suggest that vegetation cover was positively affected by this treatment, an effect which may have been lost at the highest treatment of N deposition, similar to results found by Mitchell *et al.* (2016).

4.3 Interactive effects on Collembola communities

Warming may increase the geographic range of species into areas that were previously unavailable due to climate conditions, while anthropogenic activity can further accelerate range expansion of invasive species to areas previously inaccessible due to geographic barriers. Invasive species that successfully colonise new areas are usually large generalist feeders (Smith *et al.* 2012). These characteristics describe many soil prey,

predator and microbial species. While their presence could have major consequences, few instances of invasive and native soil mesofauna interactions have been studied (but see Terauds *et al.* 2011). In Chapter 3 warming treatments and the introduction of new generalist soil predators elicited an extreme response on Collembola abundance and community composition potentially due to an increased consumptive pressure. Predator addition alone did not significantly reduce Collembola abundance but did change community composition. This may have been due to the newly introduced soil predator size selective consumption strategies, or differences in handling time due to Collembola body plan (elongated or globular).

Soil animal invasions are more difficult to study than those in terrestrial and aquatic systems but the negative interactions between invasive earthworms and native microarthropod communities are well documented (Ferlian *et al.* 2017). Invasive earthworms are differentiated by their habitat in the soil column, where they can be anecic (forming vertical burrows), euedaphic (soil dwelling) or epigeic (litter or surface dwelling) and this can affect all types of soil microarthropods. For example, Collembola interact negatively with invasive earthworms, experiencing losses in abundance through non-consumptive effects primarily due to loss of fungal hyphae networks from earthworm burrowing (Gao *et al.* 2017). Warming may be the mechanism that allows for invasive species establishment but it can also increase their metabolic costs. The newly established invasive species might offset these costs by increased foraging, exacerbating both consumptive and non-consumptive pressure on Collembola and diminishing their role in the process of decomposition. In the Boreal forest, invasive plant species are currently being facilitated due to warming and nutrient addition effects (Kent *et al.* 2018) which may further affect soil quality through changes in litter quality.

4.4 Limitations and future directions

Chapter 2 took a holistic approach where a natural boreal forest floor soil community was studied in the context of environmental change. This study had limitations in controlling for other climatic factors such as dry and wetting cycles, average seasonal temperature snow cover, aboveground vegetation and soil heterogeneity. Chapter 3 explored a

reductionist approach where forest floor soil communities were studied in the context of environmental change where factors such as soil moisture, photosynthetic processes and soil heterogeneity were carefully controlled. This study had limitations in extrapolation of observed results to variable field conditions that may exacerbate or buffer treatment effects. While both data chapters in my research had these innate limitations, they both produced similar community shift outcomes in the context of warming, inspiring confidence in the robustness of the obtained results.

Results from Chapter 2 and Chapter 3 both suggest that warming is shifting consumer community structure, which may have implications on trophic interactions to microbial and predator communities. This suggests that soil food webs may lose stability under ecological stressors and top-down effects due to abundance decreases and extreme community shifts. Soil communities are important in regulating a wide range of ecosystem processes including: carbon storage, carbon and nutrient cycling, and decomposition (Wall *et al*. 2008). Both soil communities and the ecosystem processes they perform are affected by global environmental change, which can ultimately influence global carbon dynamics (Wall *et al*. 2008).

4.5 Concluding remarks

In this thesis I demonstrated that Collembola community abundance, richness, and composition strongly respond to warming, and increased predation pressure treatments by magnifying the strength of top-down and bottom-up effects. In a three-year field experiment I established that Collembola respond to ground cable warming through shifts in community composition, but not through abundance. Community composition shifts were complemented by shifts in body size spectra, where smaller bodied Collembola were in greater abundance under warming. In a laboratory mesocosm experiment I established that both predator addition and warming treatments singly homogenize Collembola community composition and interactively homogenize composition and decrease abundance. These warming effects on communities were observed without changes in soil moisture, suggesting that new thermal regimes directly impact Collembola and predator metabolism, and potentially microbial community composition.

The consequences of warming to these belowground communities are an important note in the study of ecology and are critical to energy and nutrient cycling dynamics in soils due to climate and anthropogenic change.

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Appendices

Appendix 2.1 Collembola species abundances from the warming field experiment in Simoncouche, Quebec

Collembola species abundances (averages across all chambers) from the Lac Simoncouche warming treatment study for each destructive sampling time point. Values are average # individuals per 10 g dry weight with standard error in parentheses across the three sampling years (2015, 2016, 2017).

Lac Simoncouche	2015	2016	2017
Family Isotomidae			
Folsomia penicula (Bagnall, 1939)	20.40 (8.91)	18.41 (5.07)	30.65 (8.75)
Folsomia regularis Hammer 1953	0.08 (0.08)	0.31 (0.19)	0.07 (0.07)
Folsomia similis Bagnall, 1939	0.06 (0.06)	-	0.02 (0.02)
Folsomia sp. 1	0.10 (0.10)	-	0.66 (0.30)
Isotomidae sp. 1	-	-	0.18 (0.18)
Isotomidae sp. 2	-	0.05 (0.05)	0.03 (0.03)
Isotomurus palustris (Müller, 1776)	0.07 (0.07)	-	0.52 (0.40)
Isotomurus sp.	-	0.14 (0.08)	-
Metisotoma grandiceps (Reuter, 1891)	0.25 (0.13)	0.33 (0.23)	0.02 (0.02)
Parisotoma notabilis (Schäffer, 1896)	-	3.20 (1.28)	0.08 (0.05)
Proisotoma tenella (Tullberg, 1871)	2.24 (1.06)	2.50 (1.07)	1.74 (0.53)
Pseudosinella dubia Christiansen 1961	-	0.49 (0.40)	-
Tetracanthella ethelae Wray 1945	-	-	0.05 (0.05)
Family Entomobryidae			
Entomobryidae sp. 1	0.54 (0.24)	-	1.83 (0.98)
Entomobryidae sp. 2	0.16 (0.11)	0.06 (0.06)	0.16 (0.16)
Sinella sp.	-	0.09 (0.06)	1.04 (0.44)
Family Poduridae			
Poduridae sp.	0.26 (0.15)	0.20 (0.12)	-
Family Neanuridae			
Brachystomella parvula (Schäffer, 1896)	-	1.09 (0.35)	-
Brachystomella stachi Mills, 1934	1.16 (0.71)	1.09 (0.35)	4.06 (0.96)

Pseudachorutes simplex (Maynard, 1951)	0.14 (0.08)	0.05 (0.05)	2.07 (0.94)
Family Onychiuridae			
Onychiuridae sp. 1	1.25 (0.76)	3.93 (1.19)	2.26 (1.13)
Onychiuridae sp. 2	1.31 (0.51)	1.94 (0.67)	6.34 (1.24)
Onychiuridae sp. 3	-	3.34 (1.41)	4.28 (1.25)
Onychiurus sp. 1	1.07 (0.33)	0.89 (0.43)	8.36 (1.92)
Onychiurus sp. 2	0.07 (0.05)	0.64 (0.29)	1.74 (0.43)
Sensillonychiurus eisi (Rusek, 1976)	1.69 (0.82)	1.57 (0.43)	4.65 (0.70)
Sensiphorura sp.	-	3.96 (1.51)	1.40 (1.40)
Family Hypogastruridae			
Hypogastrura nivicola (Fitch, 1846)	0.05 (0.05)	0.34 (0.17)	0.79 (0.36)
Hypogastrura sp.	-	0.14 (0.10)	0.27 (0.16)
Tafallia sp. 1	-	-	0.23 (0.23)
Family Arrhopalitidae			
Arrhopalites incertus	0.11 (0.11)	0.17 (0.17)	0.05 (0.05)
Family Sminthuridae			
Sminthuridae sp.	0.02 (0.02)	-	-
Sminthurides sp. 1	-	0.09 (0.06)	0.28 (0.11)
Sminthurides sp. 2	-	0.14 (0.10)	-
Sphaeridia pumilis (Krausbauer, 1898)	-	-	0.08 (0.06)
Family Dicyrtomidae			
Dicyrtoma sp.	0.02 (0.02)	0.22 (0.10)	-
Family Neelidae			
Neelus (*Megalothroax*) *incertus* (Boener, 1903)	0.14 (0.08)	0.15 (0.15)	0.09 (0.07)
Family Tomoceridae			
Tomocerus sp.	-	-	0.05 (0.04)

Appendix 2.2 Collembola species abundances from the nitrogen deposition field experiment in Tirasse, Quebec

Collembola species abundances (averages across all chambers) from Lac de la Tirasse N deposition study for each destructive sampling time point. Values are average # individuals per 10 g dry weight with standard error in parentheses across the three sampling years (2015, 2016, 2017).

Lac de la Tirasse	2015	2016	2017
Family Isotomidae			
Folsomia penicula (Bagnall 1939)	4.76 (0.98)	20.18 (3.62)	23.07 (4.59)
Folsomia regularis Hammer 1953	0.38 (0.12)	14.35 (7.16)	5.09 (2.60)
Folsomia similis Bagnall 1939	0.03 (0.03)	9.07 (4.02)	-
Folsomia sp. 1	-	-	0.07 (0.07)
Folsomia sp. 2	0.13 (0.09)	0.21 (0.14)	0.05 (0.05)
Isotomidae sp. 1	0.03 (0.03)	-	-
Isotomidae sp. 2	0.16 (0.10)	-	-
Isotomidae sp. 3	-	1.21 (0.89)	-
Isotomidae sp. 4	-	-	0.66 (0.66)
Isotomurus palustris (Müller, 1776)	0.16 (0.10)	-	-
Isotomurus sp.	-	0.16 (0.11)	-
Metisotoma grandiceps (Reuter, 1891)	0.20 (0.09)	-	0.22 (0.14)
Parisotoma notabilis (Schäffer, 1896)	-	8.63 (3.12)	2.23 (0.41)
Proisotoma tenella (Tullberg, 1871)	1.32 (0.51)	7.55 (3.17)	0.35 (0.24)
Tetracanthella ethelae Wray 1945	0.07 (0.05)	-	0.09 (0.09)
Family Entomobryidae			
Entomobryidae sp. 1	0.73 (0.25)	-	-
Entomobryidae sp. 2	1.88 (0.42)	-	0.37 (0.37)
Sinella sp.	0.15 (0.14)	1.93 (1.52)	4.68 (3.23)
Family Poduridae			
Poduridae sp.	0.23 (0.12)	-	-
Family Neanuridae			
Brachystomella parvula (Schäffer, 1896)	-	1.54 (0.88)	0.09 (0.06)
Brachystomella stachi Mills,1934	0.80 (0.24)	-	0.99 (0.44)

Pseudachorutes P. simplex (Maynard, 1951)	0.09 (0.09)	0.58 (0.26)	2.16 (0.72)
Pseudachorutes sp.	-	-	0.29 (0.29)
Family Onychiuridae			
Onychiuridae sp. 1	0.41 (0.19)	1.40 (0.54)	1.39 (0.71)
Onychiuridae sp. 2	3.35 (1.04)	4.77 (2.89)	2.26 (0.66)
Onychiuridae sp. 3	0.48 (0.19)	2.84 (1.38)	1.06 (0.34)
Onychiurus sp. 1	1.16 (0.31)	5.49 (1.46)	11.55 (4.64)
Onychiurus sp. 2	-	1.17 (1.00)	1.22 (0.54)
Sensillonychiurus eisi (Rusek, 1976)	0.36 (0.14)	4.07 (2.36)	0.72 (0.35)
Sensiphorura sp.	-	0.26 (0.21)	-
Family Hypogastruridae			
Hypogastrura nivicola (Fitch 1846)	0.70 (0.70)	-	0.26 (0.13)
Hypogastrura sp.	0.10 (0.07)	0.10 (0.10)	-
Taffalia sp. 2	-	0.27 (0.27)	-
Family Sminthuridae			
Sminthuridae sp. 1	-	-	0.09 (0.06)
Sminthuridae sp. 2	0.04 (0.04)	-	-
Sminthurides sp. 1	0.07 (0.05)	0.05 (0.05)	-
Sminthurides sp. 2	0.05 (0.05)	-	-
Sphaeridia pumilis (Krausbauer, 1898)	0.03 (0.03)	0.11 (0.11)	-
Family Neelidae			
Neelus (*Megalothroax*) *incertus* (Boener, 1903)	0.05 (0.05)	0.18 (0.12)	-
Family Tomoceridae			
Tomocerus sp.	0.05 (0.05)	0.39 (0.23)	0.11 (0.07)

Appendix 3.1 Collembola abundances from Chapter 3 soil mesocosms at the start, mid-point and end of the experiment

Collembola species abundances (averages across all mesocosms) from the study for each destructive sampling time point. Values are average # individuals per 10 g dry weight with standard error in parentheses across three different time points: the initial characterization phase (T_0), at three months (T_3) and at the end of the experiment after six months (T_6).

	Pre-experiment (T_0)	Three months (T_3)	End of experiment (T_6)
Family Isotomidae			
Dagamaea tenuis (Folsom, 1934)	0.40 (0.25)	1.52 (0.32)	1.42 (0.43)
Folsomia candida Willem, 1902	0.11 (0.11)	1.36 (0.23)	1.26 (0.37)
Folsomia fimetaria (Linnaeus 1758)	0.38 (0.26)	0.40 (0.11)	0.57 (0.19)
Folsomia ozeana Yosii, 1954	1.52 (0.56)	0.81 (0.22)	1.19 (0.25)
Folsomia sp. 1	2.2 (0.68)	0.14 (0.09)	0.12 (0.05)
Folsomia sp. 2	0.16 (0.16)	0.23 (0.09)	-
Micranurophorus musci Bernard, 1977	-	1.17 (0.27)	0.64 (0.23)
Family Hypogastruridae			
Acherontiella sabina	3.28 (0.46)	1.50 (0.27)	1.51 (0.27)
Willemia sp. 1	0.52 (0.26)	2.61 (0.43)	3.86 (0.84)
Willemia sp. 2	0.9 (0.23)	2.51 (0.39)	0.2 (0.15)
Family Entomobryidae			
Entomobryidae sp.	-	0.87 (0.31)	-
Family Onychiuridae			
Onychiuridae sp. 1	0.28 (0.18)	2.3 (0.36)	2.98 (0.83)
Onychiuridae sp. 2	0.12 (0.12)	0.06 (0.04)	1.36 (0.36)
Onychiuridae sp. 3	1.01 (0.53)	0.10 (0.04)	0.12 (0.1)
Family Poduridae			
Poduridae sp. 1	0.52 (0.26)	-	-
Poduridae sp. 2	-	0.04 (0.02)	-
Poduridae sp. 3	-	0.10 (0.08)	-

Family Sminthuridae			
Sminthuridae sp. 1	-	0.72 (0.18)	0.37 (0.11)
Sminthuridae sp. 2	-	0.08 (0.03)	0.09 (0.04)
Family Dicyrtomidae			
Dicyrtoma sp.	-	0.02 (0.02)	0.19 (0.1)
Family Neelidae			
Neelides dianae	-	0.1 (0.05)	2.69 (0.78)
Neelides sp.	-	0.08 (0.03)	-
Family Tomoceridae			
Tomocerus sp.	-	0.12 (0.05)	-

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